

Environmental variables controlling soil respiration on diurnal, seasonal and annual time-scales in a mixed mountain forest in Switzerland

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Abstract Studies on soil respiration in mountain forests are rather scarce compared to their broad distribution. Therefore, we investigated daily, seasonal and annual soil respiration rates in a mixed forest (Lägeren), located at about 700 m in the Swiss Jura mountains, during 2 years (2006 and 2007). Soil respiration (SR) was measured continuously with high temporal resolution (half-hourly) at one single point ($SR_{\text{automated}}$) and periodically with high spatial resolution (SR_{manual}) at 16 plots within the study site. Both, $SR_{\text{automated}}$ and SR_{manual} showed a similar seasonal cycle. SR strongly depended on soil temperature in 2007 ($R^2 = 0.82\text{--}0.92$), but less so in 2006 ($R^2 = 0.56\text{--}0.76$) when SR was water limited during a summer drought. Including soil moisture improved the fit of the 2006 model significantly ($R^2 = 0.78\text{--}0.97$). Total annual SR for the study site was estimated as $869 \text{ g C m}^{-2} \text{ year}^{-1}$ for 2006 and as $907 \text{ g C m}^{-2} \text{ year}^{-1}$ for 2007 (uncertainty $<10\%$ at the 95% confidence interval, determined by bootstrapping). Selected environmental conditions were assessed in more detail: (1) Rapid, but contrasting

changes of SR were found after summer rainfall. Depending on soil moisture at pre-rain conditions, summer rain could either cause a pulse of CO_2 from the soil or an abrupt decrease of $SR_{\text{automated}}$ due to water logging of soil pores. (2) Two contrasting winter seasons resulted in SR being about 60–70% ($31.2\text{--}44.6 \text{ g C m}^{-2}$) higher during a mild winter (2007) compared to a harsh winter (2006). (3) Analysing SR for selected periods on a diurnal scale revealed a counter-clockwise hysteresis with soil surface temperatures. This indication of a time-lagged response of SR to temperature was further supported by a very strong relationship ($R^2 = 0.86\text{--}0.90$) of SR to soil temperature with a time-lag of 2–4 h.

Keywords CO_2 pulse · Drought · Soil CO_2 efflux · Temperate forest · Time lag · Winter respiration

Introduction

Soil respiration, the component flux of root-rhizosphere and soil microbial respiration, is the most important process of carbon loss from terrestrial ecosystems. On average, soil respiration (SR) can attribute about 70% to total ecosystem respiration in temperate forests (Janssens et al. 2001). Thus, changes in SR can strongly influence net ecosystem exchange (NEE), i.e., the balance between gross primary productivity (GPP) and ecosystem respiration

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(Valentini et al. 2000). Higher temperatures as predicted for the next decades (IPCC 2007) could increase root-rhizosphere respiration rates (Burton et al. 2008) and, of major concern, could lead to faster microbial decomposition rates of soil organic matter and thus to a positive feedback on global warming (Jenkinson et al. 1991; Davidson et al. 2000; Knorr et al. 2005; Davidson and Janssens 2006; Heimann and Reichstein 2008). However, this is still an ongoing discussion (Davidson and Janssens 2006, as other studies did not find such a clear trend of decomposition rates with mean annual temperatures (Liski et al. 1999; Giardina and Ryan 2000).

To date, SR, the second largest carbon flux in terrestrial ecosystems after GPP, has been studied in many ecosystems all over the world (Schlesinger and Andrews 2000), often in forests (e.g., Janssens et al. 2001), but mostly focusing on rather flat terrain (e.g., Longdoz et al. 2000; Pilegaard et al. 2001). However, in Switzerland, the majority of forests are located on mountainous areas, with almost half of the forests (48%) on slopes being steeper than 22° (Brassel and Brändli 1999). Despite covering about one-fourth of the forest land globally (about 9.5 million km²; UNEP-WCMC 2000), our knowledge of the magnitudes of SR fluxes in such mountain forests is rather limited. Furthermore, most often, SR measurements on mountain forest slopes are limited to the growing season (e.g., Hanson et al. 1993; Kang et al. 2003), often neglecting non-growing season fluxes. This is even more surprising, since winter soil respiration can lead to significant carbon losses from forest ecosystems, accounting for 10–20% of annual SR estimates (Zimov et al. 1996; Mast et al. 1998; Mariko et al. 2000; McDowell et al. 2000; Schindlbacher et al. 2007). Therefore, winter soil respiration can be an important factor in determining NEE, particularly in mountain forests with a pronounced snow cover (e.g., Monson et al. 2006).

Providing SR fluxes and assessing their response to climate change in any terrestrial ecosystem requires both high temporal resolution as well as spatially representative measurements over several seasons. Nowadays, these requirements are typically achieved by SR being measured either continuously with high time resolution (e.g., half-hourly) or periodically (e.g., bi-weekly) but at high spatial resolution. The calculation of annual estimates of SR linked to Eddy Covariance (EC) measurements of net

ecosystem CO₂ exchange is then done using a site-specific model, summing up modeled half-hourly or daily SR rates (e.g., Knohl et al. 2008). However, such an approach based on periodically measured SR might be biased. If measurements are not carried out frequently enough, extreme weather events might be missed or longer-lasting events such as drought undersampled and therefore not accounted properly in the respective model, resulting in under- or overestimated annual SR totals. Therefore, the combined use of continuous chamber measurements of SR with manual periodic measurements at many locations has been discussed as most beneficial, providing the most detailed picture of the response of soil respiration to environmental changes (Savage and Davidson 2003) and being the most reliable approach to gain annual SR totals. Nevertheless, studies using this combined approach to address SR in temperate mountain forests are still scarce.

Therefore, our aims were to determine the annual carbon dioxide loss from soils and to identify its dominant drivers at different temporal scales, from hourly to seasonal to interannual scales in a mixed mountain forest in Switzerland. We used a combined measurement approach with SR measured periodically at 16 plots and SR measured continuously at one single location within the footprint of an EC tower on a South-facing slope in the Swiss Jura during 2 years.

Methods

Study site and experimental setup

The CarboEurope forest flux site Lägeren (CH-LAE, 47°28'42.0"N; 8°21'51.8"E) is situated 20 km North-West of Zurich, Switzerland, at a mean altitude of about 700 m a.s.l. on the South-facing slope of the Lägeren mountain (866 m a.s.l.), part of the Swiss Jura. The study site with an altitudinal gradient of about 100 m and an average slope of 24° (45%), ranging between 10° and 45°, extends 200 m West and East, and 150 m North and South of the Lägeren EC tower and thus covers a representative area of the EC footprint (Fig. 1). The upper slope of the study site is a nature reserve and comprises a mixed beech forest unmanaged since 1998, while the lower slope is still an extensively managed forest according to

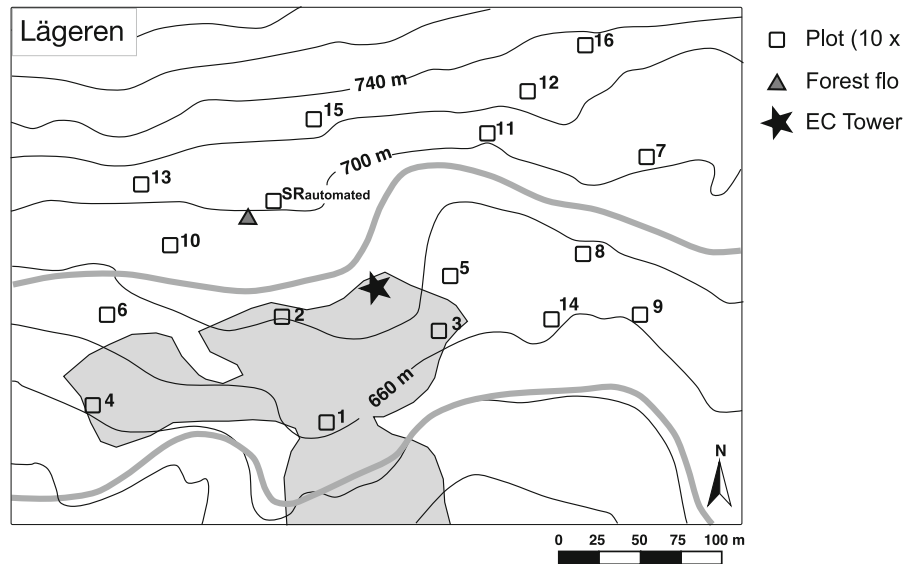


Fig. 1 Map of the Lägeren study site fully covered by forest. The locations of the plots are shown where SR_{manual} was measured bi-weekly. Plots can be identified by their numbers (see also Table 3). Continuous soil moisture was measured at the forest floor station. Air temperature and precipitation were

measured at the EC tower. Unpaved forest roads are represented by the *thick grey lines*. The *grey colored area* shows the part of the study site most affected by a winter storm in 1999 (80% of the trees were thrown)

FSC (Forest Stewardship Council) rules. The vegetation of the whole study site is typical for a highly diverse mixed mountain forest. The overstory vegetation consists mainly of beech, ash, fir, lime and spruce trees (*Fagus sylvatica* L., *Fraxinus excelsior* L., *Abies alba* Mill., *Tilia cordata* Mill., *Picea abies* (L.) Karst., respectively). These species represent over 80% of the basal area with *Quercus robur* L., *Acer pseudoplatanus* L., *Acer platanoides* L., *Carpinus betulus* L. and *Ulmus glabra* Huds. interspersed. The maximum leaf area index (LAI) of the overstory vegetation varied in the study site from 1.7 to 5.5 m⁻² over the growing seasons of the 2 years 2006 and 2007. Generally, the understory vegetation is scarce and consists mainly of *Allium ursinum* L. flowering in early spring, except for those areas that were strongly affected by a winter storm in 1999, having an often dense understory of blackberry and raspberry as well as of juvenile beech and ash trees (about 15% of the study site; Fig. 1).

The main bedrocks of the study site are limestone, marl and sandstone, with transition zones between marl and limestone (loamy debris) and marl mixed with sandstone (loam). The main soil types are rendzic leptosols (or rendzinas) and haplic cambisols according to the World Reference Base of Soil Resources

(IUSS Working Group WRB 2007). Since leaf litter decomposes almost completely within 1 year, the litter layer is distinct after autumn leaf litter fall (c. 4 cm) and decreases steadily to the end of summer (<1 cm). The rendzina soils have higher carbon (6.5 kg C m⁻²) and nitrogen (0.47 kg N m⁻²) stocks in the upper 10 cm compared to the cambisol soils (3.9 kg C m⁻², 0.3 kg N m⁻²; Heim et al. 2009; Wehrli, unpublished). Since the study site is rather heterogeneous, 17 plots (10 m × 10 m, at least 25 m apart from each other) were established, accounting for the two main soil types and associated vegetation characteristics, to ensure representativeness of the plots in the study area (Fig. 1). One litter trap of 1 m² was placed in each of the 17 plots in October 2005 within 2 m distance to the collars for SR measurements (see below). The traps were emptied monthly from October 2005 to January 2008, except during autumn sampling was intensified on a bi-weekly basis. Litter was sorted into leaves, wood and reproductive organs, dried (48 h at 65°C) and weighed. Continuous air temperature and precipitation data were available from the Swiss National Air Pollution Monitoring Network (NABEL), measured at the Lägeren EC tower. Mean annual air temperature during the two years of the study was 8.9°C in 2006 and 9.1°C

in 2007. Annual precipitation was higher in 2006 (1,032 mm) compared to 2007 (914 mm).

Automated soil respiration measurements ($SR_{\text{automated}}$)

Automated soil respiration ($SR_{\text{automated}}$) was measured during 2006 and 2007 on a half-hourly basis, in one of the plots about 50 m North-East from the Lägeren EC tower (Fig. 1), with first measurements 2 weeks after collar installation (20.3 cm inside diameter, 11 cm high, PVC). A closed system (LI-8100, Li-Cor inc, Lincoln, NE, USA), permanently connected to a chamber (Li-8100-101, Li-Cor inc, Lincoln, NE, USA) was used, opening in a 180° vertical arc to allow the soil to be exposed most of the time to ambient environmental conditions. To prevent shadow on the collar as well as precipitation exclusion on the uphill side, the open chamber was oriented to the North-East. The length of one measurement varied over the seasons: for high CO_2 efflux rates, measurement time was set to 60 s, for low CO_2 efflux rates, measurement time was expanded to 120 s. Soil temperatures (HTT thermocouple, OMEGA Engineering, Inc., Stamford, CT, USA) at 1, 5 and 10 cm depth, as well as soil moisture at 10 cm depth (EC-20, Decagon Devices Inc., Pullman, WA, USA) were logged at the same time intervals.

The zero and span gases for CO_2 and H_2O of the automated and the manual soil respiration systems were calibrated on an annual basis, since both CO_2 and H_2O zero and span calibrations showed only minor changes (drift of CO_2 span: 0.03–0.46% at 567.5 ppm) after 1 year, no data correction was applied. Data coverage of $SR_{\text{automated}}$ was about 70% in both years; in total 24,479 half-hourly measurements were included in the analysis. Data gaps occurred mostly due to equipment or power failure and after heavy snowfall when snow cover was >10 cm (lid of the LI-8100-103 did not close). In June 2006, soil cracks developed which unsealed the collar from the soil; thus, $SR_{\text{automated}}$ data were rejected, and a new collar was installed close-by (within 50 cm).

Manual soil respiration measurements (SR_{manual})

In the center of each of the 16 plots, we installed one collar, at a location without vegetation (vegetation within the collars was removed regularly), in average

about 3 m away from the nearest tree (diameter breast high >10 cm), 2 weeks prior to the measurements. The PVC collars (inside diameter of 19.6 cm, 10 cm high) were inserted about 1.5 cm into in the soil and additionally clamped with 10 cm long tent pegs to guarantee stability also at steep slopes. SR_{manual} was measured campaign-wise at all 16 plots every two to 3 weeks during 2006 and 2007, using a closed chamber system with a portable, non-dispersive infrared gas analyzer (LI-8100 with LI-8100-103 chamber, Li-Cor inc, Lincoln, NE, USA; except for measurements in January and February 2006 that were conducted with a LI-6400 with soil collars that were 10 cm in diameter and 10 cm high). During January 2006, only 11 plots could be measured due to ice on the steep slopes.

For each collar, soil respiration were measured twice; each measurement lasted on average about 90 s, separated by 60 s between repeated measurements, during which the chamber opened and closed automatically, to achieve ambient CO_2 concentrations. For later data analysis, SR_{manual} data was rejected if the coefficient of variation between the repeated measurements was >25%. In each plot, next to the SR collar, soil temperature sensors (HOBO Pendant Temperature Data Logger, Onset Computer Corporation, Bourne, MA, USA) were installed at 5 cm depth, which logged soil temperature every 30 min. All manual soil respiration measurements (SR_{manual}) were accompanied by periodical measurements of volumetric soil moisture at 6 cm depth (ML2X Theta Probe, Delta-T Devices, Cambridge, UK). These soil moisture measurements closely followed the seasonal pattern of continuous soil moisture measurements (10 cm depth; EC-20, Decagon Devices Inc., Pullman, WA, USA) at the forest floor station (Fig. 1). Thus, for later data analysis, only soil moisture measurements from the forest floor station, synchronized with SR measurements, were used.

During each SR_{manual} campaign, which lasted on average from 10 to 16 h, plots were measured in a different order to prevent confounding effects by diurnal trends. Further, potential methodological bias of the SR_{manual} campaigns could result from the time of the measurements, therefore, we compared half-hourly $SR_{\text{automated}}$ rates measured at the campaign days during 10–16 h to $SR_{\text{automated}}$ rates measured before 10 h and after 16 h at the same days. However, we found no significant differences between the

means of $SR_{\text{automated}}$ during versus before/after the SR_{manual} campaigns (paired t test: 2006, $P = 0.60$, $n = 16$; 2007, $P = 0.82$, $n = 13$). As a control for the representativeness of the measured flux rates at one fixed location (collar) per plot, we installed one additional collar at a random location within each plot. These collars were measured less frequently (c. every 2 months) and displaced after each measurement within each plot. Comparing the campaign-averages of SR_{manual} of fixed with those of randomly displaced collars, showed a strong agreement, near the one-to-one line ($rsq = 0.93$, $P < 0.001$; Fig. 2). Using a power function (see Davidson et al. 2002; Knohl et al. 2008) revealed that the campaign-averages of SR_{manual} were within 10–20% precision at a 95% confidence interval. On this basis, we considered the SR_{manual} measurements as being representative for the study site.

Soil respiration models

Soil respiration rates were related to soil temperature using a non-linear least squares model (model $SR_{m,1}$), after Lloyd and Taylor (1994):

$$SR_{m,1} = R_{\text{ref}} e^{E_0 \left(\frac{1}{T_{\text{ref}} - T_0} - \frac{1}{T_{\text{soil}} - T_0} \right)} \quad (1)$$

where R_{ref} is soil respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) under standard conditions (at $T_{\text{ref}} = 10^\circ\text{C}$; about equal to mean annual soil temperature in 5 cm depth),

E_0 (K^{-1}) is the parameter for activation energy, $T_0 = -46.02^\circ\text{C}$, as in the original Lloyd and Taylor model and T_{soil} is the measured soil temperature at a given depth.

When SR was limited by water availability, as in summer 2006, the temperature sensitivity of SR depended on soil moisture and, therefore, a second model ($SR_{m,2}$) was used, in which E_0 was defined as a linear function of soil moisture (Reichstein et al. 2003):

$$SR_{m,2} = R_{\text{ref}} e^{(aSM+b) \left(\frac{1}{T_{\text{ref}} - T_0} - \frac{1}{T_{\text{soil}} - T_0} \right)} \quad (2)$$

with SM being the measured volumetric soil moisture at a given depth, and a and b are the parameters of the linear function. The coefficient of determination (R^2) for all non-linear least squares models was calculated as:

$$R^2 = 1 - \left(\frac{\text{Residual SS}}{\text{Total SS}} \right) \quad (3)$$

whereby SS are the sums of squares. Although the theory of R^2 does not totally hold for non-linear least squared models (the residuals of non-linear least squares models do not sum up to zero; if the model totally fails, R^2 can be negative), we provide the R^2 value as an indicator for the goodness of fit for the models (Kvalseth 1985).

Annual SR estimates and uncertainties

To assess the uncertainties of modeled seasonal and annual SR estimates, caused by temporal and spatial integration, Monte Carlo simulations (parametric bootstrapping) were applied (Knohl et al. 2008). To estimate annual SR_{manual} for each plot in 2006, we first calculated the parameters R_{ref} , a and b from Eq. 2 with their respective standard deviations, using SR_{manual} (each plot) and continuous soil temperature (5 cm depth; each plot) and soil moisture (10 cm depth; forest floor station) measured at the same time. Then, 5,000 annual sums of SR_{manual} were calculated based on continuous soil temperature and moisture measurements for each plot by sampling 5,000 times triplets of the regression parameters (R_{ref} , a , b) with replacement from a trivariate normal distribution, defined by the regression parameters and the standard deviations. Based on the distribution of annual sums

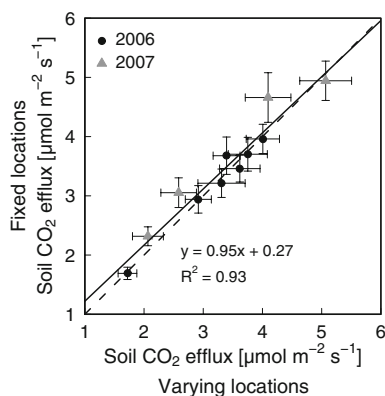


Fig. 2 Campaign-averages of SR_{manual} from fixed locations ($n = 16$) versus soil respiration from varying locations ($n = 16$) all measured within the 16 plots of the study. The linear relationship is shown by the solid black line, the dashed black line indicates the ideal one-to-one line. Bars are ± 1 SE of the means

obtained from these 5,000 samplings, we calculated the mean and 95%-confidence interval for the annual sums for each plot. To estimate the annual SR_{manual} for each plot in 2007, we followed the same procedure. First, we fitted the parameters R_{ref} and E_0 in Eq. 1 using SR_{manual} and synchronized soil temperature (5 cm depth; each plot) measurements. Then, 5,000 annual sums of SR_{manual} were calculated based on continuous soil temperature measurements for each plot by sampling 5,000 times pairs of the regression parameters (R_{ref} , E_0) with replacement from a bivariate normal distribution, defined by the regression parameters and their standard deviations. To obtain the total mean and confidence interval across several plots (e.g. for the whole study site), we averaged the annual sums from each single of these 5,000 samplings across all plots and reported the mean and 95% confidence interval of these annual SR_{manual} rates.

To gain annual or seasonal estimates for $SR_{\text{automated}}$, we had to gap-fill the data. First, we divided each year into a growing season (1 April to 31 Oct) and a dormant season (1 Jan to 31 March and 1 Nov to 31 Dec), because parameters of the Lloyd and Taylor model may change between seasons (Janssens and Pilegaard 2003). Then, we calculated the parameters of the models (Eqs. 1 and 2) with their respective standard deviations using $SR_{\text{automated}}$ with synchronized soil temperature (5 cm depth) and, if Eq. 2 was used, soil moisture measurements (10 cm depth). To estimate annual and seasonal sums as well as their uncertainties, we used Monte Carlo simulations, described above for the SR_{manual} measurements. However, uncertainties were estimated only when missing data was replaced by modeled data.

Furthermore, we analysed the influence of autocorrelation of the residual error on annual (seasonal) sums and uncertainties by recalculating all annual sums assuming no (0) and high (0.9) autocorrelation. Even if with the assumption of high (0.9) autocorrelation the effect on the annual sums and uncertainties was negligible (1%) similar as reported by Knohl et al. (2008). Hence, here we report conservative estimates of annual and seasonal SR sums and their uncertainties for $SR_{\text{automated}}$, presuming high autocorrelation of the residual error. All statistical calculations were performed using R version 2.6.1 (R Development Core Team 2007), extended by the MASS package for parametric bootstrapping (Venables and Ripley 2002).

Results

Seasonal course of soil respiration

The seasonal course of air and soil temperatures was very pronounced at our study site with lowest temperatures in January and highest temperatures in July in 2006 and 2007 (Fig. 3a, b, e, f). However, both years showed contrasting annual precipitation patterns. Spring 2006 was rather moist compared to a much drier spring 2007, while summer 2006 (June–July) was dry compared to a moist summer in 2007 (Fig. 3a, b). The SR rates measured over the 2 years showed a strong seasonal course, following changes in soil temperature (Fig. 3c, d). Using the manual approach of measuring soil respiration (SR_{manual}) to characterize the spatial heterogeneity within the study site, resulted in a minimum campaign-average of $0.41 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 1 February 2006 and a maximum campaign-average of $4.74 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 17 July 2007. In addition, using the automated approach to capture the temporal variation at one location ($SR_{\text{automated}}$), showed a minimum daily average of $0.30 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 21 January 2006 and a maximum daily average of $5.71 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 5 September 2006. Thus, SR measured with both approaches showed the same seasonal pattern (Fig. 3c, d), with the means of $SR_{\text{automated}}$ being within the range observed for the SR_{manual} measurements.

Soil respiration was typically very strongly related to soil temperature at 5 cm depth (Fig. 4). However, low precipitation (only 82.4 mm in June and July 2006, Fig. 3a) and a decline of soil moisture to a minimum of about 11% (about 40% relative soil water content, Reichstein et al. 2003) caused a strong water limitation on soil respiration. The threshold for this water limitation was at about 15% soil moisture content (about 55% relative soil water content; Fig. 4a–c). In 2006, soil temperature alone explained 76% of campaign-averages of SR_{manual} (Eq. 1, SR_{manual} : $R^2 = 0.76$, $P < 0.001$, $n = 20$; $SR_{\text{automated}}$: $R^2 = 0.56$, $P < 0.001$, $n = 12142$). Thus, taking this water limitation threshold into account and including soil moisture improved the explained annual variation of all campaign-averages of SR_{manual} in 2006 tremendously (Eq. 2, SR_{manual} : $R^2 = 0.97$, $P < 0.001$, $n = 20$; $SR_{\text{automated}}$: $R^2 = 0.78$, $P < 0.001$, $n = 12142$). In 2007, SR was strongly related to soil temperature

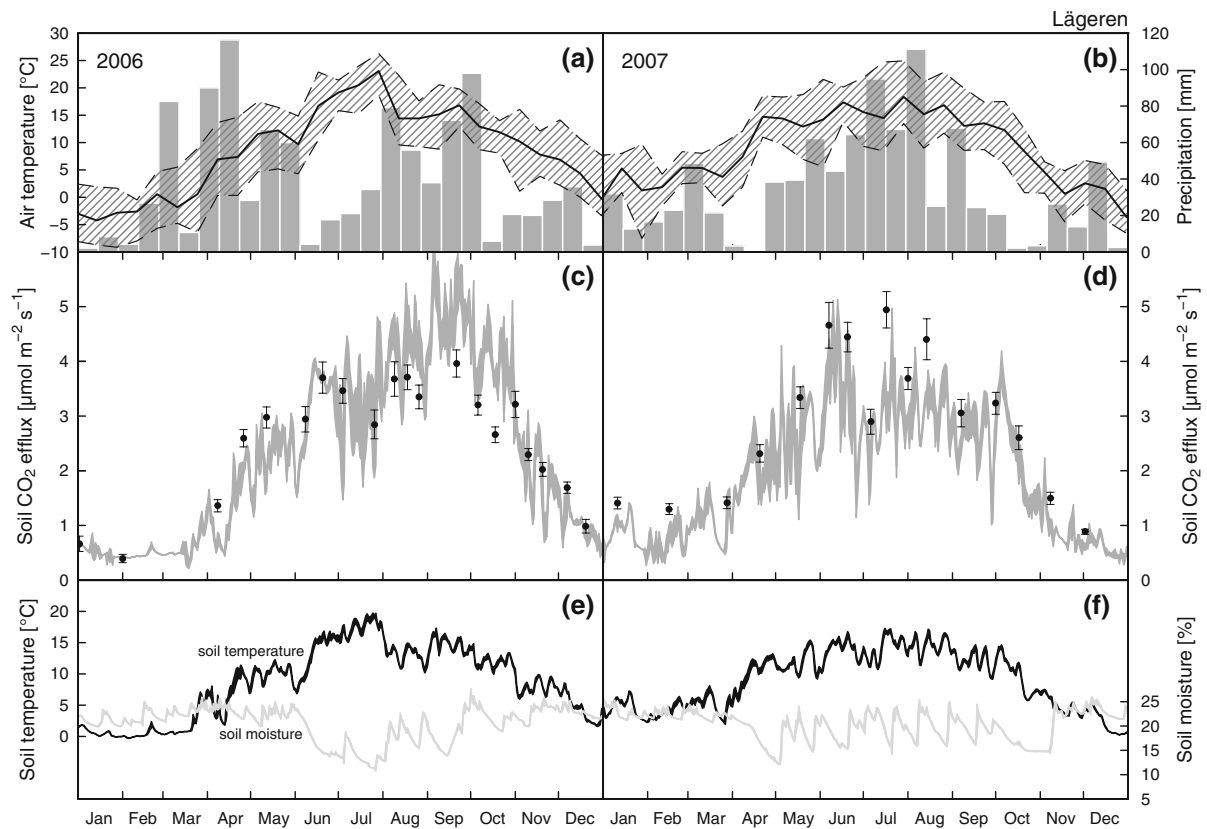


Fig. 3 Time-series of air temperature, precipitation, $SR_{\text{automated}}$, SR_{manual} , soil temperature and soil moisture for 2006 and 2007. **a, b:** air temperature averaged over 14 days is represented by the solid black line. The striped area shows the air temperature range within 14 days maximum and minimum represented by the dashed black lines. Precipitation summed over 14 days is shown by the grey barplots. **c, d:**

campaign-averages of SR_{manual} are represented by the black dots and bars (± 1 SE). Daily means of $SR_{\text{automated}}$ with standard deviations are represented by the thick grey line. Missing $SR_{\text{automated}}$ data was modeled using Eqs. 1 and 2 (see Table 1). **e, f:** daily means of soil temperature (5 cm depth) and soil moisture (10 cm depth) are shown with their respective standard deviations.

(SR_{manual} : $R^2 = 0.92$, $P < 0.001$, $n = 20$; $SR_{\text{automated}}$: $R^2 = 0.82$, $P < 0.001$, $n = 12337$; Fig. 4b and f, respectively). Even though precipitation in April 2007 was < 1 mm and soil moisture declined from 22% to about 13% (Fig. 3b, f), no water limitation on SR could be detected in 2007.

As for the data over the entire year, the dependence of half-hourly $SR_{\text{automated}}$ rates on soil temperature was also strong during dormant seasons, while it was less pronounced during growing seasons of both years (Table 1). In 2006, the temperature relationship of SR was particularly weak during the growing season (Eq. 1, $R^2 = 0.29$, $P < 0.001$, $n = 8436$), but could be substantially improved including soil moisture (Eq. 2), resulting in 59% of the variation of half-hourly $SR_{\text{automated}}$ rates being

explained (Table 1). During the growing season in 2007, only 50% of the variation of $SR_{\text{automated}}$ could be explained by soil temperature, but including soil moisture did not improve the model either.

Impact of rain events on SR in two contrasting summers

The two years of the study differed substantially in summer weather conditions. While 2006 was characterized by a drought with only 255.5 mm rain during June–August, 2007 was rather wet with 477.5 mm rain during June–August (Fig. 3a, b). This offered the opportunity to study responses of SR to rain events. During the drought spell in July 2006, when SR was water limited and soil moisture was at 13%, a strong

Fig. 4 Relationships between soil respiration and soil temperature (5 cm depth) for 2006 and 2007. The Lloyd and Taylor model (Eq. 1) and the R^2 are given for soil respiration versus soil temperature (in **a**, **c** and **e** only if soil moisture $\geq 15\%$) with the best fit indicated by the *solid lines*. The inserted smaller panels show the deviation of the model versus the best fit of the model versus soil moisture. **a**, **b**: Campaign-averages of SR_{manual} ; *bars* indicate ± 1 SE. **c**, **d**: daily-averages of $SR_{\text{automated}}$; **e**, **f**: half-hourly rates of $SR_{\text{automated}}$

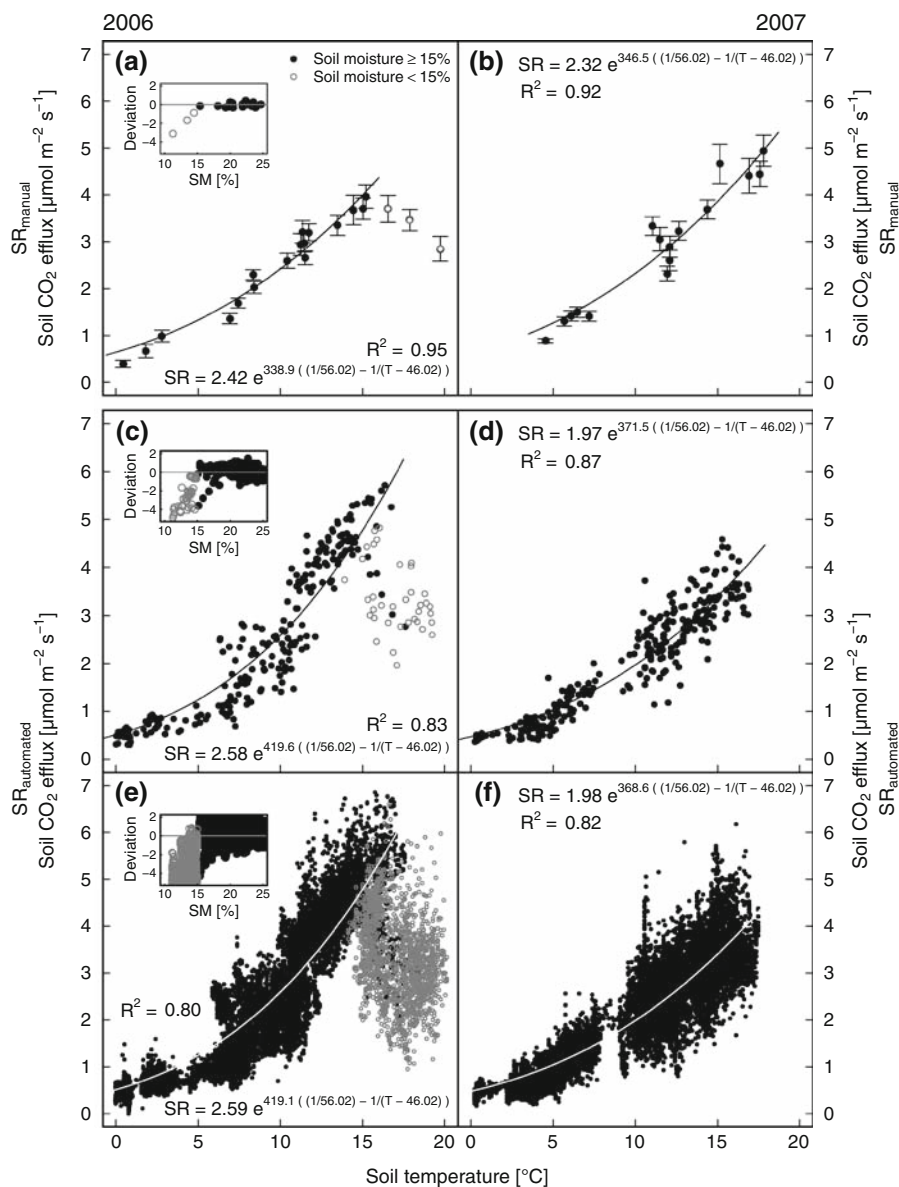


Table 1 Model parameters to gap fill $SR_{\text{automated}}$ for dormant (1 Jan to 31 March and 1 Nov to 31 Dec) and growing seasons (1 April to 31 Oct) of 2006 and 2007

Year	Season	R_{ref}	E_0	R^2	n	Model
2006	Dormant	2.44 ± 0.02	447 ± 6.57	0.67	3,706	Eq. 1
	Growing	2.69 ± 0.01	$a = 40.49 \pm 0.54$ $b = 404.38 \pm 8.51$	0.59	8,436	Eq. 2
2007	Dormant	2.29 ± 0.03	525 ± 6.57	0.61	4,523	Eq. 1
	Growing	2.15 ± 0.09	299 ± 3.65	0.50	7,814	Eq. 1

In the 2006 growing season, soil moisture (SM) was included in the model using Eq. 2. All modeled parameters were highly significant ($P < 0.001$)

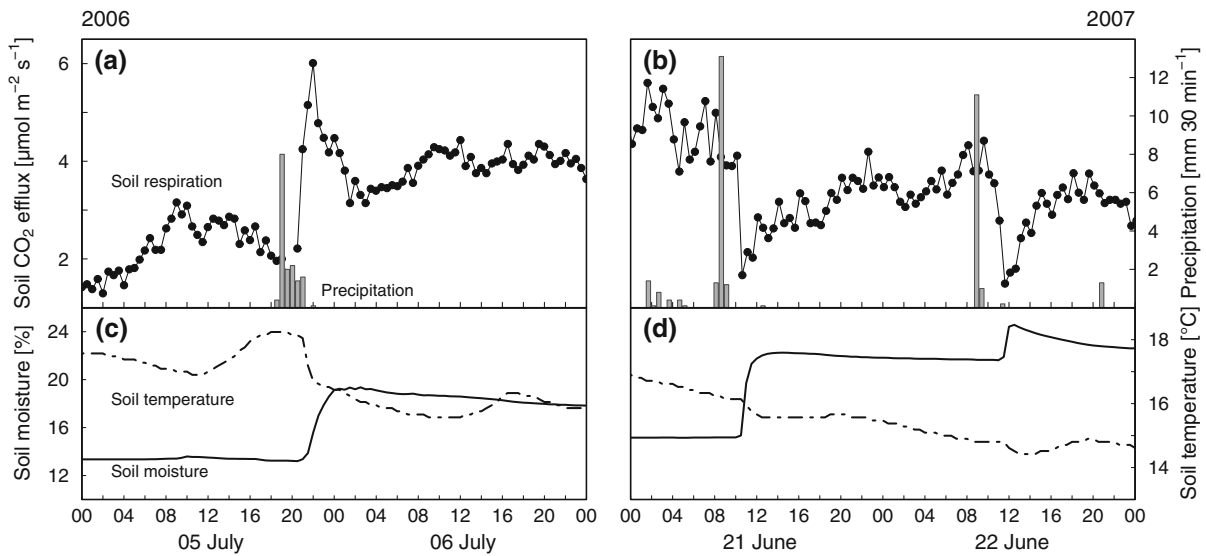


Fig. 5 Impact of heavy rain events on soil respiration. bf a, bf b: the time series of half-hourly $SR_{\text{automated}}$ and the amount of precipitation for 2006 and 2007, respectively are shown. bf c,

bf d: the time series of half-hourly soil moisture (10 cm depth) and soil temperature (5 cm depth) are given

rain event (16 mm) rewetted the soil and increased soil moisture to about 19% (Fig. 5a, c). Almost simultaneously, within 2 h, this caused a pulse of CO_2 from the soil, $SR_{\text{automated}}$ increased by a factor of 3 from about 2 to $6 \mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$ (Fig. 5a). During the following 3 h, $SR_{\text{automated}}$ rates decreased again to about $4 \mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$, but remained significantly higher than prior to the rain event. In contrast, during the wet summer of 2007, when SR was not water limited, we found a very different response of $SR_{\text{automated}}$ to very large rain events (>10 mm in 30 min). The first rain event increased soil moisture from 16 to 22%, while the second rain event increased soil moisture only slightly from 21 to 24% (Fig. 5b, d). However, in both cases, $SR_{\text{automated}}$ decreased by more than 50%, from about 4 to about $1.5 \mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$ almost instantaneously, probably caused by water logging of the soil pores. Despite such large responses of SR to individual rain events, we did not include them in the modelling of annual SR rates since such impacts of rain on $SR_{\text{automated}}$ occurred only very sporadically at our study site.

Impact of temperature on SR in two contrasting winters

Not only rain events but also cold temperature and snow affect SR during the course of a year.

Comparing the coldest months at our site, i.e., January, February and March (JFM) of 2006 and 2007, offered the opportunity to examine two contrasting winter seasons. While the harsh winter in 2006 was characterized by a distinct snow cover and air temperatures mostly below zero degrees, the winter in 2007 was rather mild with hardly any snow cover and air temperatures mostly above zero degrees (mean air temperature -1.03°C in 2006 vs. 3.96°C in 2007; mean soil temperature at 5 cm depth 1.35°C in 2006 vs. 5.04°C in 2007). On average, soil temperatures were about 4 K higher during winter 2007 than winter 2006 (Fig. 3e, f).

Since SR_{manual} measurements during JFM were not frequent enough, SR and soil temperature (5 cm) measured during the dormant season of each year was used to calculate the soil CO_2 loss during these contrasting winter seasons using Eq. 1 ($SR_{\text{automated}}$: see Table 1; SR_{manual} : 2006: $R^2 = 0.98$, $P < 0.001$, $n = 7$, $R_{\text{ref}} = 2.67$, $E_0 = 446$; 2007: $R^2 = 0.72$, $P < 0.05$, $n = 5$, $R_{\text{ref}} = 2.32$, $E_0 = 426$). The resulting cumulative flux of $SR_{\text{automated}}$ during JFM 2007 was with 80.8 g C m^{-2} (95% confidence interval of [75.3, 86.4]) about 63% higher than in 2006 with 49.6 g C m^{-2} (95% confidence interval of [39.0, 61.6]). Thus, the winter months JFM contributed about 6% in 2006, but 11% in 2007 to the annual $SR_{\text{automated}}$ estimate (see Table 2). The same pattern

was observed for the modeled cumulative flux of SR_{manual} . The carbon loss in 2007 was with 106.5 g C m^{-2} about 72% higher than in 2006 with 61.9 g C m^{-2} , while the amount of leaf litter fall during the previous autumn seasons was similar (2005: $307.5 \pm 28.4 \text{ g m}^{-2}$, 2006: $284.3 \pm 19.1 \text{ g m}^{-2}$). Thus, an increase in soil temperature of about 4 K in 2007 increased the cumulative CO_2 loss from soils by about 60–70% compared to 2006. One could speculate that a soil temperature increase of about 5–6 K might double winter soil respiration at our study site if not limited by substrate supply.

Annual soil respiration estimates

Plot-wise modeling of SR_{manual} data resulted in annual SR estimates for the footprint area ranging from 638 to $1237 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2006 and from 701 to $1290 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2007 (Table 2). In general, plots with high annual SR rates in 2006 showed also high annual SR rates in 2007. Annual averages of SR_{manual} across all plots in the study site were not significantly different in 2006 ($869 \text{ g C m}^{-2} \text{ year}^{-1}$) compared to those in 2007 ($907 \text{ g C m}^{-2} \text{ year}^{-1}$), as well as leaf litter input did not differ between the 2 years (Table 2). Variations among the 16 plots in SR were large, but could not be explained by differences in mean annual soil temperature, maximum LAI, leaf litterfall or fine root biomass (data not shown). Comparing the two different soil types present at our site using a *t* test, we found no significant differences in annual SR rates, although leaf litter fall was significantly higher for the rendzina soils than for the cambisol soils (2006: $t = -4.64$, $P < 0.001$; 2007: $t = -3.70$, $P = 0.002$). The annual $SR_{\text{automated}}$ estimate was $868 \text{ g C m}^{-2} \text{ year}^{-1}$ for 2006, well within the 95% confidence interval of the annual SR_{manual} estimate for our study site. However in 2007, the annual $SR_{\text{automated}}$ estimate of $729 \text{ g C m}^{-2} \text{ year}^{-1}$ was about 20% lower than the SR_{manual} estimate (Table 2).

Diurnal variations of soil respiration

Diurnal variations of SR calculated as differences between daily maximum and daily minimum values varied during the course of the years. In general, periods with greater diurnal variations in $SR_{\text{automated}}$ rates coincided with high daily temperature

variations. Monthly averaged diurnal variations of $SR_{\text{automated}}$ for the two study years increased linearly with monthly averaged diurnal variations of air temperature ($R^2 = 0.78$, $P < 0.001$), but less so with soil temperature (1 cm depth: $R^2 = 0.43$, $P < 0.01$; 5 cm depth: $R^2 = 0.40$, $P < 0.01$).

To learn more about the relationships between diurnal variations of $SR_{\text{automated}}$ rates and soil temperatures, we selected periods using the following criteria: (1) periods with more than 10 days of continuous soil respiration data, (2) pronounced diurnal variation of surface soil temperature (1 cm depth) $> 1.5 \text{ K}$, and (3) no major rain event ($< 5 \text{ mm}$ in 30 min). Only four periods met these strict criteria: 07–27 July 2006 (July), 14–27 August 2006 (Aug), 01–25 September 2006 (Sep) and 15 April to 3 Mai 2007 (April). During these periods, the diurnal variations of surface soil temperature were quite pronounced (1.8–3.3 K), decreasing with soil depth to about 0.6 K at 10 cm. At the same time, diurnal variations of SR were about $0.4\text{--}0.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, with lowest SR rates between 9–12 h and highest SR rates between 17–19 h, following the course of soil temperature with some delay (Fig. 6b–h). However, this was not the case during the July 2006 period, when SR was water limited (Fig. 6a, e). During this period, SR increased during the night, while soil temperatures still decreased. Therefore, a counterclockwise hysteresis of SR was found after plotting $SR_{\text{automated}}$ against soil temperature for Aug, Sep and April (Fig. 7a), i.e., the soil respiration rates lagged soil temperature (1 cm depth) by several hours and were generally higher during the night compared to the day at the same soil temperature (Fig. 7a, grey dot represents SR at 1:00 h). To further test the hypothesis of a time-lag in SR to soil temperature, we investigated the relationships of $SR_{\text{automated}}$ shifted forward between 0 and 12 h with soil temperature at different depths using Eq. 1, and compared the models with Akaike's Information Criterion (Table 3). While the relationship between non-lagged SR (0 h forward shift) and soil temperature in 1 cm depth was weak (R^2 between 0.04 and 0.36), the strength of the relationship increased with depth where soil temperature was measured (R^2 between 0.48 and 0.83). However, also the temperature sensitivities increased, resulting in unrealistic high temperature sensitivities of SR with $E_0 > 1,000 \text{ K}^{-1}$ for soil temperatures at 10 cm depth (data not

Table 2 Site characteristics are given by plot name (Plot), leaf are index (LAI), dominant tree species (Tree species) and numbers of tree species (#) in Plots 1–10 on cambisol soils and in Plots 11–16 on rendzina soils

Plot	LAI	Tree species	#	2006						2007					
				Litter	ST	n	R ²	R _{ref}	annual SR	Litter	ST	n	R ²	R _{ref}	annual SR
1	1.7	<i>Quercus robur</i> ^a	2	286	10.03	19	0.76	2.73	1032 [927, 1136]	412	10.25	16	0.57	1.86	783 [578, 975]
2	2.2	<i>Fagus sylvatica</i> ^a	2	309	10.15	20	0.86	2.35	904 [803, 1006]	378	9.96	16	0.91	2.23	901 [834, 965]
3	2.5	<i>Fagussylvatica</i> ^b	3	192	9.37	19	0.84	1.67	655 [575, 730]	233	9.48	16	0.80	1.94	752 [659, 847]
4	3.1	<i>Abies alba</i> ^a	2	340	9.22	18	0.73	3.22	1075 [968, 1186]	322	9.55	15	0.79	2.88	1,128 [984, 1,277]
5	3.2	<i>Abiesalba</i> ^b	2	255	9.20	20	0.81	2.34	857 [764, 953]	294	8.97	16	0.89	2.58	1,075 [946, 1,200]
6	5.1	<i>Abies alba</i>	2	317	8.76	18	0.87	2.70	866 [792, 942]	231	9.45	16	0.84	2.05	847 [731, 960]
7	5.2	<i>Fraxinus excelsior</i>	4	301	8.36	20	0.87	2.92	954 [881, 1029]	398	8.87	16	0.91	2.49	1,137 [1,043, 1,235]
8	5.5	<i>Abies alba</i>	2	383	8.50	20	0.75	2.55	790 [705, 882]	408	8.87	16	0.88	2.49	922 [834, 1,010]
9	5.9	<i>Acer pseudoplatanus</i>	2	275	8.69	20	0.89	2.10	735 [674, 795]	360	9.72	16	0.81	1.88	701 [619, 787]
10	6.0	<i>Fraxinus excelsior</i>	4	288	8.80	20	0.54	2.20	758 [654, 873]	363	9.14	16	0.61	2.36	878 [708, 1,044]
11	4.7	<i>Fraxinus excelsior</i> ^a	4	436	8.82	20	0.84	3.38	1,237 [1,091, 1,379]	443	9.56	13	0.67	3.06	1,290 [895, 1,657]
12	5.5	<i>Picea abies</i>	5	485	8.47	19	0.78	2.63	789 [724, 858]	499	9.01	16	0.65	2.36	865 [741, 996]
13	3.7	<i>Fraxinus excelsior</i>	2	426	8.89	19	0.86	2.07	638 [586, 695]	521	9.46	16	0.85	1.89	751 [655, 845]
14	4.7	<i>Fagus sylvatica</i>	3	460	9.08	19	0.92	2.72	949 [889, 1010]	629	10.40	16	0.85	2.43	973 [853, 1,093]
15	2.3	<i>Fagus sylvatica</i>	1	370	9.86	18	0.86	2.13	805 [713, 898]	400	10.70	16	0.80	1.87	796 [701, 888]
16	3.8	<i>Fraxinus excelsior</i>	2	345	8.89	20	0.86	2.18	815 [736, 898]	406	9.72	16	0.90	2.09	826 [745, 910]
Cambisol	4.1	<i>Abies alba</i>	10	295	9.06				867 [838, 894]	340	9.37				901 [864, 938]
Rendzina	4.1	<i>Fraxinus excelsior</i>	9	420	9.00				872 [837, 908]	483	9.81				917 [843, 989]
All	4.1	<i>Fagus sylvatica</i>	10	342	9.04				869 [846, 890]	394	9.53				907 [871, 942]
SR _{automated} ^c	5.2	<i>Fraxinus excelsior</i>	3	446	8.60				868 [837, 900]	390	8.86				729 [709, 748]

For each plot annual leaf litter (g m⁻²), mean soil temperature in 5 cm depth (ST), model results (n, R², R_{ref}) and annual SR (g C m⁻² year⁻¹) received by parametric bootstrapping are given for 2006 and 2007, respectively. Averaged soil temperature (ST) as well as annual SR estimates calculated by averaging each sampling of the parametric bootstrapping from the models on plot level for cambisol, rendzina and all plots are shown. The 95% confidence intervals for the annual SR estimates are given within squared brackets

Vegetation of understorey: ^a *Fagus sylvatica*, ^b *Fraxinus excelsior*, ^c for model results see Table 1

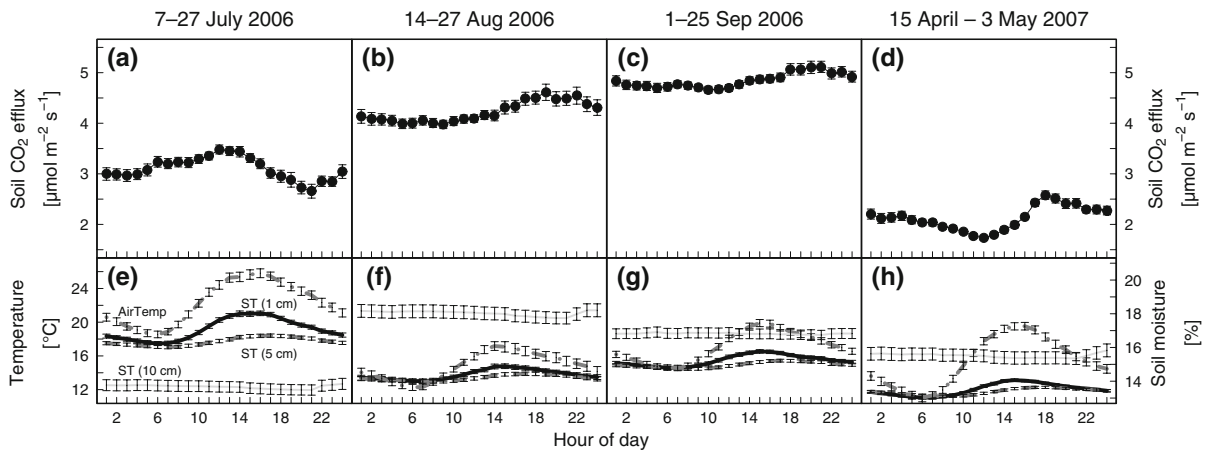


Fig. 6 Diurnal variations of soil respiration for selected periods. Shown are hourly rates of $SR_{\text{automated}}$ averaged over the respective period in 2006 and 2007 (a–d). Hourly air

temperature (AirTemp), soil temperature (ST) in 1 and 5 cm depth as well as soil moisture in 10 cm depth are also given (e–h). Bars are ± 1 SE

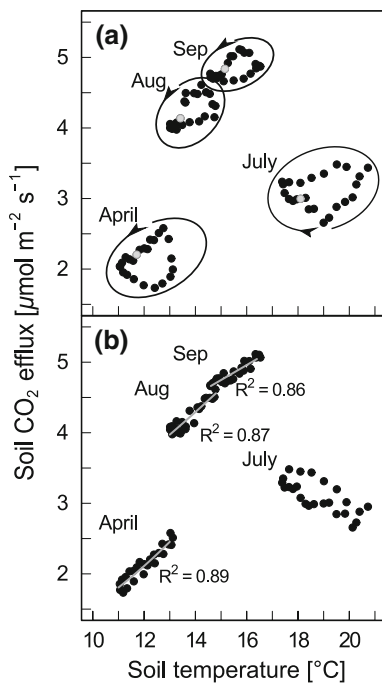


Fig. 7 Diurnal variations and time-lag of soil respiration versus soil temperature for selected periods. Hourly $SR_{\text{automated}}$ rates averaged over the periods 7–27 July 2006 (July), 14–27 August 2006 (Aug), 1–25 September 2006 (Sep) and 15 April to 03 May 2007 (April) are plotted against soil temperature (1 cm depth). In **a** SR at 1:00 h is represented by the grey dots and the direction of the hysteresis is indicated by the arrows. In **b** $SR_{\text{automated}}$ is plotted with a time lag of 4 h versus soil temperature (SR lagging soil temperature) and the R^2 of the relationship, as well as the best fit are given by the solid grey lines (Eq. 1)

shown). Comparing all regression models, the best fit (smallest AIC) of SR to soil temperature was found for SR with a 2–4 h lag compared to soil temperature at 1 and 5 cm depth. With a 4 h time lag, the hysteresis of SR with soil temperature disappeared (Fig. 7b). For the drought period in July 2006, we found a clockwise hysteresis, i.e., the diurnal course of SR was lagged by soil temperature (Fig. 7a, b). To investigate the consequences of these findings over longer time scales, we analysed $SR_{\text{automated}}$ data (dormant and growing season) assuming time lags of SR of 1–4 h. However, the thereby resulting models did not improve in comparison to the models from Table 1. Thus, the time lag of SR to soil temperature was not consistent at shorter and longer time periods but occurred only when diurnal variations of surface soil temperatures were pronounced.

Discussion

Seasonal course of soil respiration

Highly different seasonal and diurnal courses of SR were observed during 2006 and 2007 in a mixed mountain forest on a South-facing slope in the Swiss Jura. Soil respiration could be modeled using soil temperature as single predictive variable with a high coefficient of determination, if soil water was not limiting (Fig. 4). Including soil moisture into the

Table 3 Coefficients of determination for non-lagged and lagged diurnal variations of soil respiration with soil temperature in 1, 5 or 10 cm depth (ST) for the three periods: 14–27 August 2006 (Aug 06), 01–25 September 2006 (Sep 06), and 15 April to 03 May 2007 (April 07)

	R^2 for non-lagged soil respiration			R^2 for lagged soil respiration		
	ST (1 cm)	ST (5 cm)	ST (10 cm)	ST (1 cm)	ST (5 cm)	ST (10 cm)
Aug 06	0.36	0.71	0.83	0.90 ^{(3)a}	0.89 ⁽²⁾	0.74 ⁽¹⁾
Sep 06	0.23	0.65	0.83	0.86 ⁽⁴⁾	0.87 ^{(2)a}	0.85 ⁽¹⁾
April 07	0.04 ^{n.s.}	0.48	0.73	0.89 ^{(4)a}	0.87 ⁽²⁾	0.83 ⁽¹⁾

Only the R^2 of the best fit (smallest AIC) of time lagged $SR_{\text{automated}}$ is given for each soil temperature; numbers in parenthesis indicate the hours of the time lag (all regressions were significant ($P \leq 0.05$) if not otherwise stated)

^a Best fit over all temperatures

model (Eq. 2) allowed us to predict SR rates also very accurately during the 2006 summer drought. However, not all temporal variations in SR could be explained by soil temperature and soil moisture, indicating that temporal variations of SR were coupled to further environmental drivers such as substrate availability, photosynthesis and precipitation (Kirschbaum 2004; Tang et al. 2005a; Buchmann et al. 1997).

Impact of rain events on soil respiration

It is commonly observed in many ecosystems that SR can be enhanced after rain (e.g. Birch 1958; Lee et al. 2004; Jarvis et al. 2007) although other authors report SR being suppressed when soil pores become water logged (e.g. Buchmann et al. 1997; Bowden et al. 1998; Hirano et al. 2003). However, to our knowledge, this is the first study in which both contrasting effects of rain on SR were observed within one ecosystem. Rapid rewetting after soil drying often yields a pulse of CO_2 from the soils (Birch 1958; Xu et al. 2004; Jarvis et al. 2007). Different reasons could come into play: (1) The replacement of CO_2 rich soil air by rain water could explain this pattern. However, assuming a CO_2 concentration of 2000 ppm in soil air and CO_2 evolving from the upper 20 cm of the soil, the replacement of 6% of soil air would have created a pulse of $0.6 \mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$ during 30 min, directly after soil rewetting. (2) Most probably, soil microbes are responsible for producing this pulse, due to mineralization of destabilized soil organic matter during drying and rewetting cycles, or due to additional mineralization of microbial C, which becomes

available after microbial cell lyse and/or by the release of osmoregulatory solutes (e.g., Fierer and Schimel 2003; Jarvis et al. 2007). Such pulses of CO_2 can significantly alter the net annual carbon gain of Mediterranean ecosystems (Jarvis et al. 2007). However, this is very unlikely for our study site as these pulses were very scarce.

On the other hand, SR can also be suppressed by moderate to high soil moisture, because CO_2 diffusion out of the soil and O_2 diffusion into the soil are limited, decreasing aerobic autotrophic and heterotrophic respiration. In a soil incubation experiment, Bowden et al. (1998) found that SR increased with increasing soil moisture, but declined at water holding capacity $>80\%$. In our study, we observed a fast decrease of $SR_{\text{automated}}$ of about 50% after a strong rain event ($>10 \text{ mm}$ in 30 min) at moderate soil moisture conditions (16%). The same response was observed in an Amazonian rainforest, where SR rates were found to decrease by about 40% after heavy rain (Buchmann et al. 1997). Similar findings are also reported from a deciduous forest in Japan, where SR was measured continuously using a CO_2 concentration profile (Hirano et al. 2003). After rain, diffusion was low, CO_2 concentration increased in the soil pore space and SR decreased by about 15% during and directly after the rain event. This comparatively small reduction could be due to the less intense rain event ($<5 \text{ mm h}^{-1}$) and the low respiration rates before rain. In general, the direct effects of summer rain on SR observed in our study might be of concern for those measuring SR manually to generate models, since measurements made after such rain events could significantly bias modelled seasonal or annual soil respiration.

Winter soil respiration

During winter, when tree activity is strongly reduced, SR is typically dominated by heterotrophic respiration (Tang et al. 2005b; Schindlbacher et al. 2007; Ruehr and Buchmann submitted), thus increasing winter temperatures mainly enhances decomposition of litter and soil organic matter. Winter air temperatures (January–March) at our study site were about 5 K higher during the mild winter in 2007 compared to the harsh winter in 2006, while soil temperature (5 cm depth) increased only by 4 K, probably due to snow cover and its thermal insulation of the soil. Nevertheless, carbon dioxide loss increased by about 60–70% from winter 2006 to winter 2007, most likely due to enhanced microbial decomposition caused by higher temperatures since substrate availability estimated from leaf litter fall and its species composition (data not shown) of the two previous autumn seasons (2005 and 2006) were very similar. The SR rates measured during both winter seasons at soil temperatures below 5°C were in good accordance to other studies in forest ecosystems (e.g., Hirano 2005; Schindlbacher et al. 2007).

Since temperate ecosystems act as a carbon source to the atmosphere during winter periods (e.g., Malhi et al. 1999), monitoring winter carbon loss will become more important in a warmer world. In subalpine forests, the amount of carbon lost during winter can be as much as 50–90% of the carbon gained in the previous summer (Monson et al. 2005). For our study site, the longterm (1987–2007) mean air temperature during January to March is about 1.5°C. In the future, a mild winter like the one in 2007 might become more regular, as a temperature increase of about 0.9–3.4 K is predicted for this region until 2050 (OcCC 2007). However, the effects of increasing temperatures on litter and soil organic matter decomposition and their potential feedback on climate change are still a matter of debate (Davidson and Janssens 2006). On the one hand, soil respiration is thought to be more sensitive to temperature than primary production, and thus climate warming should increase the net loss of carbon from soils to the atmosphere (Jenkinson et al. 1991). On the other hand, decomposition rates could also become limited due to depletion of readily decomposable substrate

(Kirschbaum 2004). However during winter, a large amount of easily decomposable organic matter is typically available to soil microbes after leaf litter fall in temperate deciduous and mixed forests, therefore decomposition should not be limited by substrate availability but rather by temperature in these forests. Thus, enhanced carbon loss from soils of mixed and deciduous mountain forests is very likely in future winters.

Annual soil respiration estimates

Despite pronounced differences in temperature and precipitation during winter and summer seasons of the two study years, mean annual temperatures and amounts of precipitation as well as annual SR_{manual} rates were comparable between the two study years. While we found annual SR_{automated} rates in 2007 to be about 15% lower compared to 2006 (and 20% lower than annual SR_{manual} rates in 2007). This decrease in SR_{automated} rates could have probably resulted from a “chamber installation effect”, since we did not change the location of the collar and the chamber since June 2006. The Li-8100-101 chamber is mounted on a frame to hold free from the soil surface. But this frame is still covering the soil surrounding the collar by about 5 cm wide just like a tiny roof. When the chamber is open (c. 90% of the time) another about 350 cm² of the adjacent soil is covered. This might have reduced precipitation and litter input to the soil, and thereby contributed to the lower estimates of SR_{automated} in 2007.

Nevertheless, the Lägeren forest lost on average about 900 g C m⁻² year⁻¹ via soil respiration during the two study years (Table 2; with an uncertainty <10% at the 95% confidence interval), well within the range of estimates of other beech-dominated forests in Europe (Table 4), except the youngest (Hesse) and the most Northern forest (Lille Boegeskov), which had much lower annual SR rates. Compared to a spruce dominated forest (Weidenbrunnen), comparable in altitude and stand age to our study site, the beech forests showed much higher annual SR rates, due to vegetation type, higher mean annual temperature and/or to differences in SR measurement techniques (Table 4). These findings indicate that similar processes underlay SR in beech-dominated forests on mountain slopes as on flat terrain.

Table 4 Annual estimates of soil respiration for beech and mountain forests in Europe

Site	Elevation (m a.s.l.)	Slope (%)	Age (years)	Temp (°C)	Precip (mm)	Period	SR	References
Lägeren (CH) ^{a, c}	700	45	50–150	8.4	930	2006 2007	869 907	This study
Collelongo (I) ^{a, c}	1,550	–	90	7.4	1,100	1996–1997	879	Matteucci et al. (2000)
Vielsalm (BE) ^{a, c}	450	3	60–90	7.5	1,000	1997–1998	870	Longdoz et al. (2000)
Hainich (D) ^{a, c}	445	3–5	0–250	7.8	800	2000 2001 2002	908 919 896	Knohl et al. (2008)
Hesse (F) ^{a, c}	300	0–5	30	9.2	820	1996 1997	575 663	Epron et al. (1999)
Lille Boegeskov (DK) ^{a, d}	40	0	80	8.1	600	1996 1997	368 457	Pilegaard et al. (2001)
Weidenbrunnen 2 (D) ^{b, c}	760	2	112	6.0	1,019	1997 1998 1999 2000	497 566 592 586	Subke et al. (2003)

Elevation, average slope, mean stand age, air temperature (Temp) and precipitation (Precip) as well as annual soil respiration estimates ($\text{g C m}^{-2} \text{ year}^{-1}$) are given

–, no prevalent slope, variable topography

^a Overstory dominated by *Fagus sylvatica*

^b Overstory dominated by *Picea abies*

^c Closed chamber (manual)

^d Closed chamber (campaign-wise automatic)

^e Open chamber (semi-automatic)

Time lags of SR vs. soil temperature

During periods when SR was not water-limited, a pronounced counterclockwise hysteresis between SR and surface soil temperature was observed, similar to a study from Gaumont-Guay et al. (2006) for a boreal aspen forest. In their study, soil respiration peaked 3.5–5 h later than soil temperature at 2 cm depth while soil moisture did not change over the day. However, they did not find SR to lag soil temperature at 10 cm depth, but similar to our study—an unusually high temperature sensitivity—of this relationship ($Q_{10} > 150$) was reported. Such an unrealistic temperature sensitivity of SR arises because CO_2 production from the upper soil layers is compared to a relatively small temperature change in 10 cm depth. Therefore, we argue that surface soil temperature (1–5 cm depth) is most suitable to model diurnal variations in $\text{SR}_{\text{automated}}$ with a time-lag of 2–4 h (if respiration is not limited by water availability).

The reason for the observed lag of SR to soil temperature could either be (1) a physically driven process from the production of CO_2 to its diffusion from the soil surface (e.g., Jassal et al. 2004), (2) a biologically driven process caused by direct supply of the root-rhizosphere with recently assimilated carbon as some studies indicate (e.g., Tang et al. 2005a) or (3) a combination of physical and biological processes (Riveros-Iregui et al. 2007). At our study site, photosynthesis reached its maximum at around midday (S. Etzold 2008, *personal communication*), 6–8 h earlier than $\text{SR}_{\text{automated}}$. A similar pattern was found in an oak-grass savanna where the peak in SR lagged photosynthesis by about 7–12 h (Tang et al. 2005a). Tang et al. (2005a) concluded that the short time lag may not be due to the real transport of carbohydrates in the phloem translocation stream, but due to the propagation of pressure and concentration fronts, which arrive much faster in the sink organs than in the solution itself (Thompson and Holbrook 2004).

For a montane conifer forest, Riveros-Iregui et al. (2007) found the degree of hysteresis between soil CO₂ production and soil temperature to decrease with declining water content during the growing season. In contrast, we found still a strong hysteresis effect under water-limited conditions, although in the opposite, clockwise direction (i.e., SR increased before soil temperature) during the drought spell in July 2006. Then, SR_{automated} increased during the night (when soil temperature decreased) and peaked at midday. The reasons are less clear: Trees mostly refill their stem water reserves during night, when transpiration is low. Water uptake during night can also lead to hydraulic redistribution of soil water from deeper and moister soil layers to the more shallower drier soil via the root system (Caldwell et al. 1998) and could therefore increase both root-rhizosphere and microbial respiration (see Carbone et al. 2008). Using dendrometers at an ash tree next to the SR_{automated} measurements (within 2 m), we observed a distinct diurnal variation of the trunk diameter during the drought period in July 2006. Tree trunk diameter increased during the night until the next morning, caused mainly by water uptake and storage, followed by a decrease in the late morning due to enhanced transpiration (Ruehr, unpublished data). However, no significant change of soil moisture was seen during the diurnal cycle (Fig. 6), suggesting that only the water content of roots and their adjacent rhizosphere was enhanced which could not be detected in the bulk soil where soil moisture was measured. Thus, increasing nighttime SR during the 2006 summer drought might be the result of water redistribution from deeper soil layers to shallower fine roots, which would cause root-rhizosphere respiration to increase. However, to provide further evidence detailed research on soil-plant water interactions is needed.

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