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Carbon losses due to soil warming: Do autotrophic and heterotrophic soil respiration respond equally?

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Abstract

Global warming has the potential to increase soil respiration (R_S), one of the major fluxes in the global carbon (C) cycle. R_S consists of an autotrophic (R_A) and a heterotrophic (R_H) component. We combined a soil warming experiment with a trenching experiment to assess how R_S, R_A, and R_H are affected. The experiment was conducted in a mature forest dominated by Norway spruce. The site is located in the Austrian Alps on dolomitic bedrock. We warmed the soil of undisturbed and trenched plots by means of heating cables 4 °C above ambient during the snow-free seasons of 2005 and 2006. Soil warming increased the CO_2 efflux from control plots (R_S) by ~45% during 2005 and ~47% during 2006. The CO_2 efflux from trenched plots (R_H) increased by ~39% during 2005 and ~45% during 2006. Similar responses of R_S and R_H indicated that the autotrophic and heterotrophic components of R_S responded equally to the temperature increase. Thirty-five to forty percent or $1\,t\,C\,ha^{-1}\,yr^{-1}$ of the overall annual increase in R_S ($2.8\,t\,C\,ha^{-1}\,yr^{-1}$) was autotrophic. The remaining, heterotrophic part of soil respiration ($1.8\,t\,C\,ha^{-1}\,yr^{-1}$), represented the warming-induced C loss from the soil. The autotrophic component showed a distinct seasonal pattern. Contribution of R_A to R_S was highest during summer. Seasonally derived Q_{10} values reflected this pattern and were correspondingly high (5.3–9.3). The autotrophic CO_2 efflux increase due to the 4 °C warming implied a Q_{10} of 2.9. Hence, seasonally derived Q_{10} of R_A did not solely reflect the seasonal soil temperature development.

Keywords: autotrophic soil respiration, carbon, forest, heterotrophic soil respiration, Q_{10}, soil warming, temperature sensitivity

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Introduction

The CO_2 release from soil (soil respiration; R_S) is one of the major fluxes in the global carbon cycle and exceeds the release of CO_2 due to anthropogenic combustion processes by an order of magnitude (Marland *et al.*, 2006; IPCC, 2007). R_S consists of an autotrophic (root and rhizosphere respiration; R_A) and a heterotrophic [decomposition of soil organic matter (SOM); R_H] component. Both forms of respiration are temperature sensitive (e.g. Lloyd & Taylor, 1994; Bååth & Wallander, 2003). Therefore, global warming stimulates R_S and increases the carbon flux from the soil to the atmosphere (Davidson *et al.*, 2000; Rustad *et al.*, 2001; Melillo *et al.*, 2002). Increasing the rate of R_S can weaken the C sink strength of terrestrial ecosystems and even turn them into C sources (Cox *et al.*, 2000; Jones *et al.*, 2003; Canadell *et al.*, 2007). Forests in the Northern hemisphere are currently an important terrestrial carbon sink (Goodale *et al.*, 2002; Janssens *et al.*, 2003a). Temperate and boreal forests contain huge stocks of soil C (Dixon *et al.*, 1994). Enhanced mineralization of these SOM stocks could have a strong impact on future atmospheric CO_2 concentrations.

SOM occurs in labile forms, for example, as fresh litter or root exudates and more stable to almost recalcitrant forms such as complex humic substances bound to clay minerals. For an understanding of warming effects on SOM decomposition and R_S, it is necessary to understand how the different C pools respond to warming. Great effort was made to assess whether labile and stabile SOM pools differ in their temperature sensitivities (Melillo *et al.*, 2002; Fang *et al.*, 2005; Knorr

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et al., 2005; Reichstein *et al.*, 2005). In a literature review, Davidson & Janssens (2006) suggested a wider view. They established that the decomposition of SOM is determined by substrate availability and several environmental variables that are often lumped to an 'apparent temperature sensitivity'. Simultaneously, a number of studies highlighted that active C transport from plants had a strong influence on the forest soil CO_2 efflux (Campbell *et al.*, 2004; Yuste *et al.*, 2004; Göttlicher *et al.*, 2006; Scott-Denton *et al.*, 2006; Sampson *et al.*, 2007). As much as half of the soil respiratory release can be derived from recent photosynthate (Hanson *et al.*, 2000; Högberg *et al.*, 2001).

With warming increasing the total CO_2 efflux from soil, it is interesting to understand how the autotrophic and the heterotrophic components of R_S are affected. Warming effects on R_A may not directly influence the soil C pool because R_A is closely linked to C gain by photosynthesis. However, R_A and R_H are difficult to separate because of the complex interaction between heterotrophic decomposers, mycorrhizae, and plant roots (Hanson *et al.*, 2000; Kuzyakov, 2006). Recent techniques gave insights in C transport from the canopy to the roots and allowed a reliable quantification of R_A and R_H (Kuzyakov, 2006; Heinemeyer *et al.*, 2007; Högberg *et al.*, 2008). Further, progress was made to better understand how soil temperature affects R_A and R_H (Boone *et al.*, 1998; Bååth & Wallander, 2003; Bhupinderpal-Singh *et al.*, 2003; Irvine *et al.*, 2005). However, it remains difficult to draw conclusions about warming effects on forest soil C dynamics by combining the results of different studies that either focus on a separation of R_A and R_H or on soil temperature effects.

In the present study, we combined a soil warming experiment with a trenching experiment. The experimental design allowed us to separate R_A and R_H, and to quantify the soil warming effect on R_S, R_H, and R_A. We increased the soil temperature by means of heating cables by 4 °C compared with the ambient soil temperature at 5 cm soil depth. A global mean temperature rise by 4 °C over the next 100 years is within the projections of the IPCC (A2 Scenario) (IPCC, 2007). However, there is strong evidence that air temperatures in the Alps increase even faster (Christensen & Christensen, 2007; Rebetez & Reinhard, 2007).

In contrast to most other soil warming studies, our site is on calcareous bedrock (approximately 35% or $\sim$ 1.4 million ha of Austria's forest). In previous soil warming studies on silicate bedrock, the warming effect on CO_2 emissions declined when the pool of readily decomposable substrate was exhausted (Kirschbaum, 2006; Hartley *et al.*, 2007). Soils derived from dolomitic limestone have low contents of oxides and clay minerals and therefore major mechanisms of soil C stabilization are absent. We hypothesize that under the site conditions of our experiment, soil warming leads to a stronger and longer lasting increase in R_S than observed in previous soil warming experiments on sites with silicate bedrock (Rustad & Fernandez, 1998; Rustad *et al.*, 2001; Strömgren, 2001; Melillo *et al.*, 2002).

Materials and methods

Site description

The study site is located in the Northern Limestone Alps at 910 m a.s.l. on a north–northeast slope of a mountain in western Austria (47°34′50″N; 11°38′21″E). The field site is characterized by a cool humid climate with maximum precipitation in summer. Snow-free period is from April/May to November/December. Mean annual air temperature and precipitation were 5.7 °C and 1480 mm [(1987–2007; Zentralanstalt für Meteorologie und Geodynamik (ZAMG))], respectively. The experimental forest is 120 years old and is dominated by Norway spruce (*Picea abies*), with interspersed silver fir (*Abies alba*) and European beech (*Fagus sylvatica*). The soils are a mosaic of shallow Chromic Cambisols and Rendzic Leptosols. The bedrock is formed of dolomite. Soils are characterized by high carbonate content and have a near neutral pH and a high biological activity (Härtel *et al.*, 2002). Mull is the dominant humus form and the depth of the O layer does not exceed 3 cm. The A horizons reach 40 cm in Rendzic Leptosols and 10–20 cm in Chromic Cambisols. Root density is highest in the O and A horizons, and few roots are found as deep as 60 cm. A detailed description of the site is given in Herman *et al.* (2002).

Experimental design

In 2004, three experimental plots were randomly set on the site. Each of the three plots was divided into five 2 × 2 m subplots. Subplot 1 was warmed by heating cables. Subplot 2 served as disturbed-control plot. Here, we inserted cables that were later not heated, but had inflicted the same soil disturbance as on the warmed subplot. Subplot 3 served as untreated control. Around subplots 4 and 5, we dug trenches and cut off all roots. One of the trenched subplots was warmed in the same manner as subplot 1.

A 1 m wide buffer strip was kept between control and warmed subplots to avoid warming of control plot's soil. No stems were located in the subplots.

Soil warming

In autumn 2004, six subplots (three warmed, three trenched-warmed) were equipped with resistance heating cables (0.4 cm diameter, TECUTE – 0.18 $\Omega\,m^{-1}$ UV^{-1}, Etherma, Salzburg, Austria). The cables were buried in 3 cm deep slots and had a spacing of 7–8 cm. A preliminary experiment had shown that 7.5 cm distance between the cable lines ensured homogenous soil warming at an intercable temperature difference of $<0.5\,^{\circ}C$. The warming system was controlled by a datalogger (Campbell CR 10; Campbell Scientific Inc., North Logan, UT, USA). Each of the three plots was controlled separately by two temperature sensors (PT100; Kucera, Brno, Czech), which were inserted on warmed and control subplots. The sensors were placed in the mineral soil at a depth of 5 cm halfway between two cable lines on the warmed subplots and randomly at 5 cm mineral soil depth on the control subplots. Whenever the temperature difference between two adjacent subplots (warmed, control) was less than 4 °C, a heating transformer (primary 230 Vac/50 Hz, secondary 40V, 79, 2A; UMS, Munich, Germany) was activated to supply the heating cables with electricity. Whenever the temperature difference exceeded 4 °C the controlling datalogger shut the heating transformer down. We assumed that the soil temperature development of the trenched subplots was similar to the temperature development of the adjacent nontrenched subplots. Hence, for reasons of technical simplicity, the warming of the trenched subplots was operated in series with the warming of the nontrenched subplots.

We started the soil warming in July 2005 and warmed until a snow cover built up. In 2006, soil was warmed throughout the snow free season. In both seasons, soil warming was prolonged 1 week after initial snow cover built-up. Hence, the warmed subplots stayed snow-free for 1 more week than the control subplots.

Trenching

We trenched the subplots in 2004. Trenches were dug around 2.5 m × 5 m plots and reached down to solid bedrock at 30–80 cm depth. Roots in the trenches were cut. Root ingrowth was inhibited by insertion of a plastic lining. The sparse understory vegetation was removed repeatedly from the trenched plots. Each trenched plot was divided into two subplots (2 m × 2 m). One of the subplots was equipped with heating cables. The subplots were placed in the outermost positions allowing 1 m spacing between the heated and the control plots.

CO_2 flux measurements

During the snow-free season, CO_2 fluxes were measured fortnightly. Three plastic chambers (20 cm diameter, 10 cm height) were placed randomly on each of the 15 subplots. The chambers were inserted 1 cm into the soil in order to ensure an airtight seal. A plastic strip was spanned around each chamber and the chamber was secured with three 20 cm long steel hooks. This design provided stability to the chamber during the CO_2 measurements and prevented dislocation of the chambers. The chambers were not shifted during the experiment. CO_2 efflux was measured with a closed dynamic system. For each CO_2 flux measurement, a chamber was closed with a stainless steel lid. The lid had a round rubber sealing to ensure a gas tight connection between the chamber and the lid and a vent to prevent over- or underpressure in the chamber headspace. Attached to the lid was a WMA-4 infrared gas analyzer (PP-Systems, Hitchin, UK; closed system, flow rate of 0.4 $L\,min^{-1}$). Each chamber was closed for 3 min. The chamber headspace CO_2 concentration was recorded every 20 s. R_S was calculated from the linear headspace CO_2 concentration increase over the last 2 min. Soil respiration measurements of all 45 chambers took nearly 4 h. To assure a consistent measurement protocol, we started the CO_2 flux measurements between 9:00 and 10:00 hours and measured the same sequence from chamber 1 to 45 starting with plot 1 and ending with plot 3. Within plots, the chambers were allocated randomly between treatments. The analyzer was calibrated every month using pure N_2 for zero calibration and a standard gas (500 ppm CO_2; Linde, Vienna, Austria). In winter, the CO_2 efflux was calculated from snow-CO_2 concentration profiles (Schindlbacher *et al*., 2007).

Environmental parameters and soil solution analysis

Each subplot was equipped with PT100 temperature sensors and ECH_2O-10 soil moisture probes (Decagon, Washington, USA) at 5 and 15 cm mineral soil depths. Temperature and moisture sensors of heated subplots were placed halfway between adjacent cable lines. Soil temperature and moisture on all subplots were recorded every 30 min and the data were stored on two Delta-T DL2 dataloggers (Delta-T Devices Ltd., Cambridge, UK). ECH_2O-10 soil moisture probes were calibrated for the soil properties at our experimental site in the laboratory by inserting them into an undisturbed soil block (50 cm × 50 cm × 40 cm) that was gradually dried. The soil block was placed on a balance and the weight was continuously recorded. We finally dried the soil at 105 °C, determining the soil bulk density, and calculated the volumetric water contents.

The C export in the aqueous phase was estimated from a model-based simulation of the seepage rate and measured concentration of dissolved organic carbon (DOC) in the soil solution (Jandl *et al*., 2002). Water samples were collected with 10 ceramic suction cups

(SK 48; UMS). Suction cups were installed at one plot only. They were placed at 15 and 30 cm depths at each subplot. A pressure of −1.7 bar was maintained by a vacuum pump. The pump was activated in 6 h intervals. Soil water samples were collected in 1 L glass bottles, which were emptied every second week. Samples were filtered through a 0.45 µm membrane filter and DOC was analyzed with a Shimadzu TOC 5050 (Shimadzu Corp., Japan). The DOC concentration in the calcareous gravel at 30 cm depth of the mineral soil represents the chemical quality of the seepage water. Multiplication of the water flux out of this soil horizon with the DOC concentration yields an estimate of the DOC flux density.

Data analysis

The contribution of autotrophic soil respiration (R_A) was estimated as the difference between R_S from control plots and R_H obtained from trenched plots. The apparent temperature sensitivities of R_S, R_H, and R_A were described by means of a Q_{10} function (Janssens & Pilegaard, 2003b):

$$R = R_{10} \times Q_{10}^{((T-10)/10)}, \qquad (1)$$

where R, the dependent variable, is the measured soil CO_2 efflux, R_{10} the simulated soil respiration at 10 °C, Q_{10} the temperature sensitivity of the soil respiration (the respiratory flux at one temperature over the flux at a temperature 10 °C lower), and T, the independent variable, is the soil temperature. The R_{10} and Q_{10} were fitted to the measured R and temperature data by means of a nonlinear least-square fitter (SIGMAPLOT for Windows, Version 10; SyStat Software Inc., Germany).

The actual warming effects on R_S and R_H were calculated as the differences between the mean CO_2 efflux from disturbed-control and warmed subplots. The actual effect of soil warming on R_A was estimated by subtracting the differences in CO_2 fluxes from disturbed-control/trenched subplots from the differences in CO_2 fluxes from warmed/trenched-warmed subplots.

To ensure the comparability of CO_2 fluxes, measured CO_2 fluxes were corrected where soil temperature diverged on trenched and nontrenched plots during the CO_2 flux measurements. When soil warming on trenched plots deviated from the desired 4 °C difference, we corrected the measured values with a simple model. The model [Eqn (2)] is derived from CO_2 fluxes of warmed-trenched plots during 2005 and 2006 (Fig. 1).

$$CO_2\ \text{flux} = 1.537 \times 2.774^{(T-10)/10}, \qquad (2)$$

where T is the control-trenched soil temperature in 5 cm depth plus 4 °C. To test the model performance, we modelled CO_2 fluxes at the actual temperatures of the warmed-trenched plots in 2006 (T is the temperature of warmed-trenched plots) as well and found a good fit (coefficient of determination = 0.90). Especially in the later part of 2006, when the experimental warming was less than 4 °C above the control, the modelled R_H was almost similar to the measured R_H ($R^2 = 0.95$).

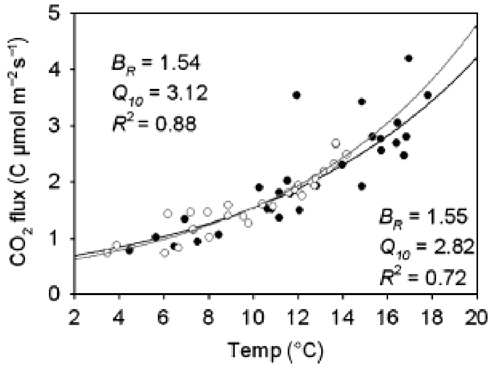


Fig. 1 Relationship between soil temperature and mean CO_2 efflux ($n = 3$) from trenched plots (open circles, grey curve) and warmed-trenched plots (full dots, black curve) during 2005 and 2006. Parameters of the fitted Q_{10} function for warmed-trenched plots (black) were used in Eqn (2). The functions and Q_{10} values of the treatments do not differ significantly.

Moreover, we needed to account for differences in soil moisture at control and trenched plots. We used data from an incubation experiment (Schindlbacher *et al.*, 2008) to quantify the effect of soil moisture on soil respiration. The incubation study was conducted with soil samples from trenched and nontrenched subplots that were collected in early December 2005. Soil samples were incubated at a constant soil temperature of 15 °C and soil water contents ranging from 12 to 74 vol% soil moisture. CO_2 fluxes were measured automatically. The best fit to the data ($R^2 = 0.97$) was obtained with the following cubic function :

$$\begin{aligned} CO_2\ \text{flux} = & -3.276 + 0.7486 \times \text{vol\%} \\ & - 0.01533 \times \text{vol\%}^2 + 0.00008015 \times \text{vol\%}^3 \end{aligned} \qquad (3)$$

The function showed optimal conditions for soil respiration between 25 and 45 vol% soil moisture. At wetter and dryer conditions, soil respiration decreased and reached zero levels at 4 and 75 vol% soil moisture, respectively (Schindlbacher *et al.*, 2008). We first modelled the trenched subplot CO_2 efflux and the control subplot CO_2 efflux at 15 °C [Eqn (3)]. Then we used the relative difference to correct the CO_2 efflux at the actual soil temperature.

Estimates of annual and seasonal soil C losses were made by linear interpolation between sequential CO_2 flux measurements in our time series (Sigmaplot, procedure AREA). The effect of soil warming on the CO_2 efflux was tested statistically by repeated measures ANOVA (SAS Institute Inc., Cary, NC, USA). The CO_2 efflux was strongly correlated ($R^2 = 0.90$) to the depth of the humus layer and the A horizon of the three plots. Hence, we weighted the CO_2 flux measurements by the average humus layer depths of the three plots (3, 1.5, and 2.1 cm) in order to increase the power of the repeated measures ANOVA. Differences between treatments were tested during soil warming in 2005 and 2006 ($P < 0.05$). For 2005, we additionally tested for interactions within time and treatment ($P < 0.05$). Therefore, we compared the mean CO_2 fluxes of each treatment and plot before warming (2 months), with the first 2 months of warming and the second 2 months of warming. Maulchy's test was used to assess sphericity. If the assumption of sphericity was violated, we corrected using Greenhouse–Geissler ($\varepsilon < 0.75$) or Huynh–Feldt ($\varepsilon > 0.75$) estimates.

Results

Soil temperature

The warming experiment started in July 2005. The elevated soil temperature was reached during the day after turning on the heating (Fig. 2a and b). Soil temperatures of the warmed subplots stayed close to 4 °C above control subplot temperatures for the following month (Fig. 2b). Two plots were overheated during 3 weeks in August 2005. On the third plot, the temperature difference of 4 °C was maintained. Soil temperatures of the overheated plots were irreproducible because the datalogger produced erroneous readings during this time. As plus 10 °C was found to be the maximum heating capacity during a short-term warming experiment in late 2005 (Schindlbacher *et al.*, 2008), overheated plot soil temperature may have been increased by about 10 °C as well. From August to October 2005, the soil temperature difference of 4 °C was held constant except for a week in late October when power supply problems occurred. At the end of November, the warming was stopped for the season. In 2006, warming commenced immediately after the snow cover disappeared and continued flawless for the entire season (Fig. 2b). During both seasons, soil warming increased the soil temperatures at 15 cm mineral soil depth by 2.5–3 °C (Fig. 2b). The warming effect at 15 cm soil depth showed a similar temporal trend as the warming effect at 5 cm depth but was delayed by 4–6 h.

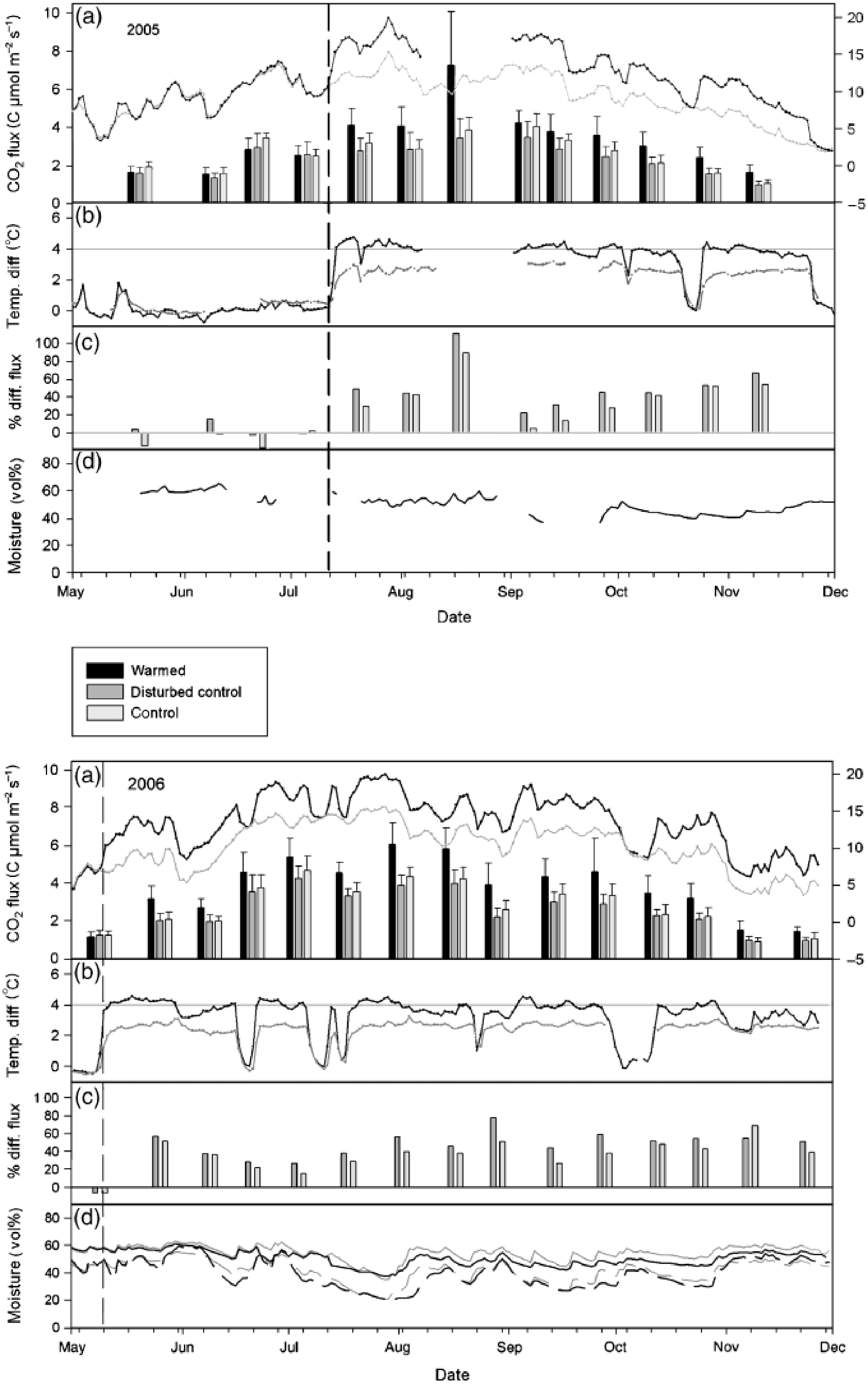
Soil temperature development was similar on trenched-control subplots and on control subplots. The mean daily soil temperatures for the sampling days during 2005 were 10.23 ± 0.70 °C for control plots and 10.14 ± 0.71 °C for trenched control plots. During 2006, mean daily soil temperatures for sampling dates were 9.78 ± 0.87 °C for control and 9.80 ± 0.88 °C for control-trenched plots. Soil warming on trenched subplots was operated in series with soil warming on nontrenched subplots but the temperature difference on trenched subplots temporarily diverged from the desired 4 °C at 5 cm soil depth. Especially in 2006, the 4 °C difference between trenched-control and trenched-warmed could not be maintained for most of the season (Fig. 3). Two trenched subplots were overheated during 3 weeks in August 2005 as well.

Soil moisture

Soil moisture was underestimated by approximately 40% when calculated with the default calibration equation of the $ECHO_2$-10 moisture probes. A site-specific equation was derived from the lab calibration.

The seasonal development of soil moisture on non-trenched plots is shown in Fig. 2d. In 2005, control plot soil moisture at 5 cm mineral soil depth was highest (65 vol%) in spring and remained at high levels until a short dry period in September. In 2006, soil moisture at 5 cm soil depth was high in spring and autumn and decreased in summer. The lowest value (21 vol%) was recorded at the end of July. Soil moisture at 15 cm soil depth varied between 37 and 61 vol% on warmed plots and between 35 and 63 vol% on control plots. Control plot soil moisture at 15 cm soil depth was on average 2.0

Fig. 2 (a) Annual soil temperature development at 5 cm soil depth on control plots (grey line) and warmed plots (black line). Bars show the mean CO_2 efflux (black: warmed, dark grey: disturbed-control, grey: control) ± SE ($n = 3$) during the snow free season in 2005 (top) and 2006 (bottom). (b) Mean daily soil temperature differences between warmed and control plots at 5 cm (black line) and 15 cm (grey line) soil depth. (c) Relative difference between CO_2 efflux from warmed and disturbed-control plots (dark grey bars) and between warmed and control plots (grey bars). (d) Seasonal development of daily mean soil moisture at 5 cm soil depth (dashed black: warmed, dashed grey: control) and at 15 cm soil depth (solid black: warmed, solid grey: control). Vertical dashed lines indicate the beginning of soil warming.


(a)
2005
CO$_2$ flux (C µmol m^{-2} s^{-1})
Soil temp. 5 cm (°C)
(b)
Temp. diff (°C)
(c)
% diff. flux
(d)
Moisture (vol%)
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Date
Warmed
Disturbed control
Control
(a)
2006
CO$_2$ flux (C µmol m^{-2} s^{-1})
Soil temp. 5 cm (°C)
(b)
Temp. diff (°C)
(c)
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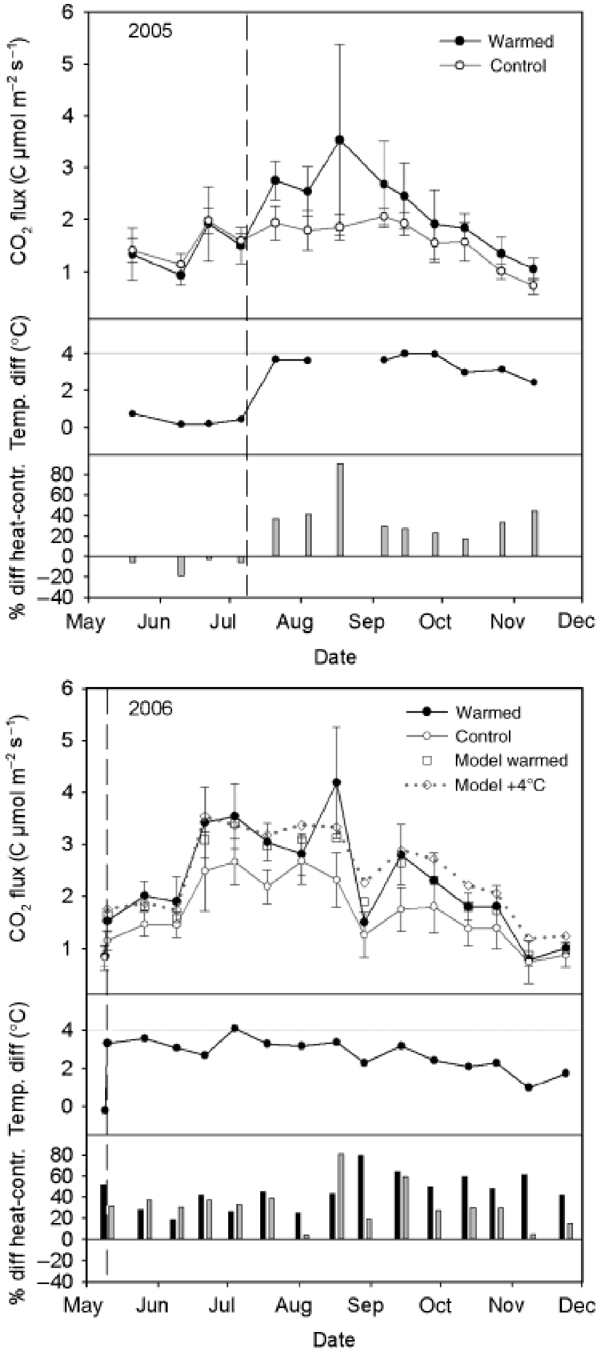

Fig. 3 Mean CO$_2$ efflux from trenched and warmed trenched plots during 2005 and 2006 ± SE ($n = 3$) and modelled CO$_2$ efflux at actual trenched warmed plot temperatures and at control plot temperature + 4 °C for 2006 (top). Mean daily temperature difference between trenched and warmed trenched plots (middle). Relative differences between trenched and trenched-warmed plot CO$_2$ efflux (grey bars) and between trenched plot CO$_2$ efflux and CO$_2$ efflux modeled at trenched plot soil temperatures + 4 °C (black bars). Vertical dashed lines indicate the beginning of soil warming (bottom).

(± 0.2) vol% higher than soil moisture of warmed plots during 2006. At 5 cm soil depth, control plot soil moisture was on average 0.2 (± 0.2) vol% higher than soil moisture of warmed plots. Soil moisture at warmed and control plots showed similar development throughout 2006 (Fig. 2d).

Soil moisture content on trenched subplots was high throughout both seasons. Mean daily soil moistures at 5 cm soil depth varied between 48 and 64 vol% in 2005 and between 45 and 56 vol% in 2006. Soil moisture at trenched and control subplots was similar in spring and autumn but differed during summer when soil moisture at trenched subplots stayed at high levels (Fig. 4).

CO$_2$ efflux

CO$_2$ efflux from the three plots showed high spatial variability throughout both seasons. The coefficient of variation during 2005 varied between 12% and 67%. In 2006, the coefficient of variation varied between 21% and 66%. CO$_2$ efflux from disturbed-control subplots tended to be slightly lower than the CO$_2$ efflux from untreated control subplots during 2005 and 2006 (Fig. 2). The difference was statistically not significant. However, the differences between control and disturbed-control CO$_2$ fluxes showed a strong relationship to the seasonal development of R_A (Fig. 5).

Soil warming significantly increased the CO$_2$ efflux from warmed plots compared with disturbed-control plots during both seasons (2005: $P = 0.004$, Fig. 2a; 2006: $P = 0.018$, Fig. 2b). Further, a significant time-by-treatment interaction during 2005 ($P = 0.028$) proved the positive warming effect. The high CO$_2$ flux (7.26 µmol m^{-2} s^{-1}) from warmed plots in mid-August 2005 was the mean flux of two subplots that were overheated in that period and the flux from one subplot that was heated by 4 °C. After setting the temperature difference at all plots back to 4 °C, the difference in CO$_2$ efflux from warmed and control subplots declined and increased again during autumn (Fig. 2a). The average CO$_2$ efflux from warmed subplots in 2005 (excluding CO$_2$ measurements from overheated plots in August) was 45 ± 5% (SE, $n = 8$) higher than the mean CO$_2$ efflux from disturbed-control plots and 33 ± 6% higher than the CO$_2$ efflux from control plots. During 2006, the average CO$_2$ efflux from warmed subplots was 47 ± 3% (SE, $n = 16$) higher than CO$_2$ efflux from disturbed-control subplots and 40 ± 3% higher than CO$_2$ efflux from control subplots.

CO$_2$ fluxes from trenched plots were consistently lower than CO$_2$ fluxes from control plots. The difference varied throughout the seasons. Measured differences between R_S and R_H were highest between August and October during both seasons (Fig. 4). When corrected

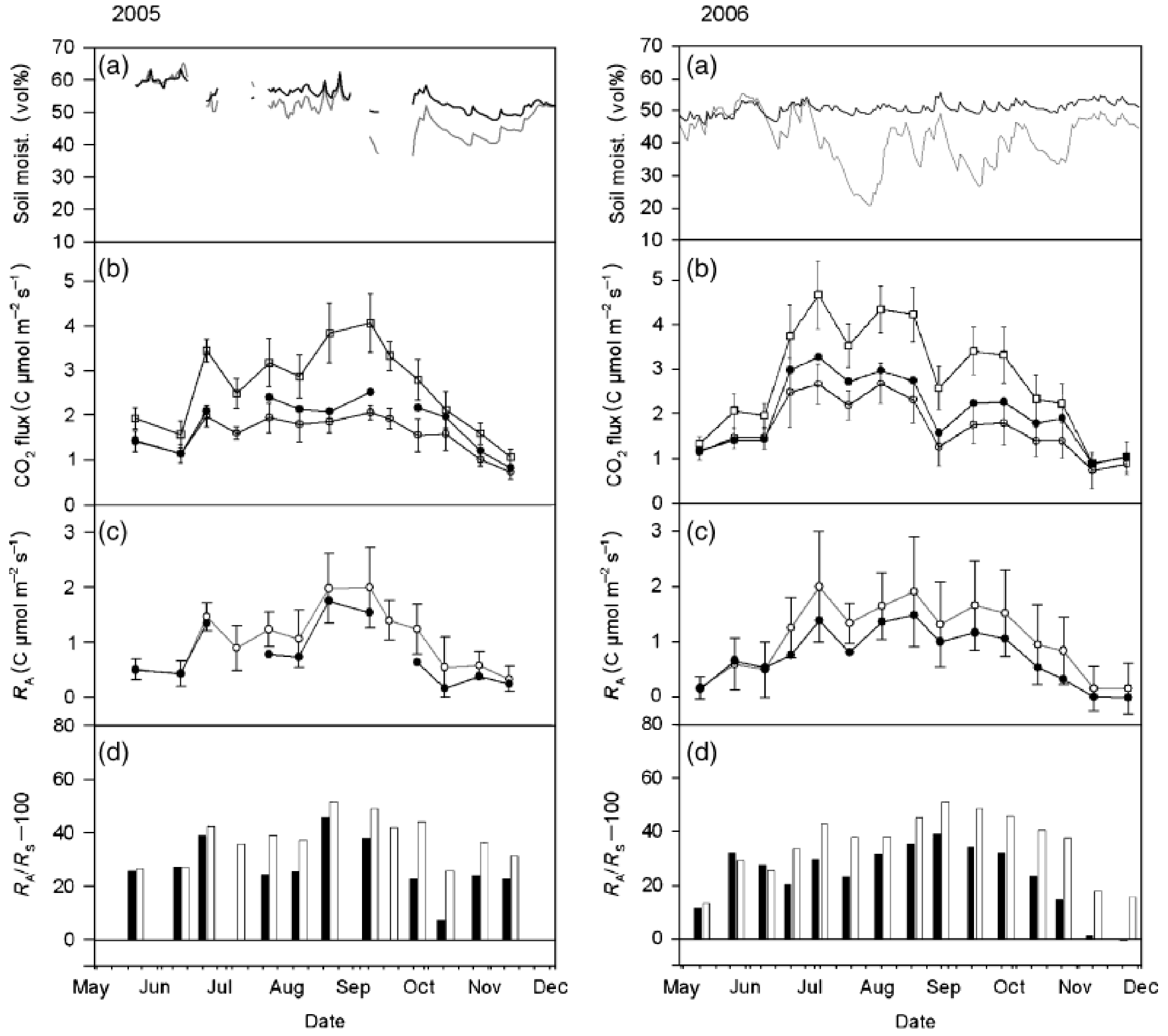

Fig. 4 (a) Development of mean daily soil moisture at 5 cm soil depth on control (grey line) and trenched plots (black line). (b) Mean CO_2 fluxes ± SE ($n = 3$) from control plots (squares), trenched plots (open circles), and from trenched plots but corrected for differences in soil moisture (full dots). (c) R_A estimated from original R_H data (open circles) and estimated from soil moisture corrected R_H data (full dots). (d) Relative contribution (%) of R_A to R_S (white bars for original data, black bars for moisture corrected data).

for differences in soil moisture, R_H increased in the majority of cases resulting in lower R_A (Fig. 4). Corrected for soil moisture, R_A was highest in spring and summer during 2005 and 2006 but decreased sharply during autumn 2006. Mean measured contribution of R_A to R_S (control plot CO_2 efflux minus trenched-control plot CO_2 efflux) was 38% and 35% for 2005 and 2006, respectively. When corrected for differences in soil moisture, the mean contribution of R_A to R_S was 28% and 24% for 2005 and 2006, respectively.

Soil warming on trenched plots increased the CO_2 efflux as well. The temporal variability was higher than on nontrenched plots (Fig. 3). Excluding the artefacts of the overheating episode, in 2005 soil warming on trenched plots increased the average CO_2 efflux by 39 ± 3% (SE, $n = 8$) compared with the CO_2 efflux from trenched-control plots. In 2006, actual soil warming, varying between 1 and 4 °C, increased R_H on average by 33 ± 5% (SE, $n = 16$). When corrected by Eqn (2) (modelled for a constant 4 °C warming), R_H was on average increased by 45 ± 5% during 2006. Soil warming increased the estimates of R_A on average by 75 ± 15% (SE, $n = 9$) during 2005 and by 56 ± 13% during 2006 (SE, $n = 15$).

Table 1 shows Q_{10} values of R_S, R_H, and R_A. Q_{10} values of R_A exceeded other Q_{10} values during both seasons. Especially in 2005, Q_{10} values of R_A were explicitly high. Q_{10} values of trenched plot CO_2 fluxes tended to be lower than Q_{10} values for control plot CO_2 fluxes during both seasons.

DOC flux

The DOC concentrations at 30 cm soil depth ranged from 3 to 30 mg C L^{-1} during the 2006 growing season. The highest concentrations were measured in September and October. The annual water flux density below 30 cm was 1150 mm with a maximum in autumn. The total outflux of DOC was 3.1 g C m^{-2} (disturbed-control), 1.6 g C m^{-2} (warmed), 2.7 g C m^{-2} (trenched + trenched-warmed). Because of the coincidence of the maximum DOC concentrations and maximum water flux densities, the DOC export was highest in autumn.

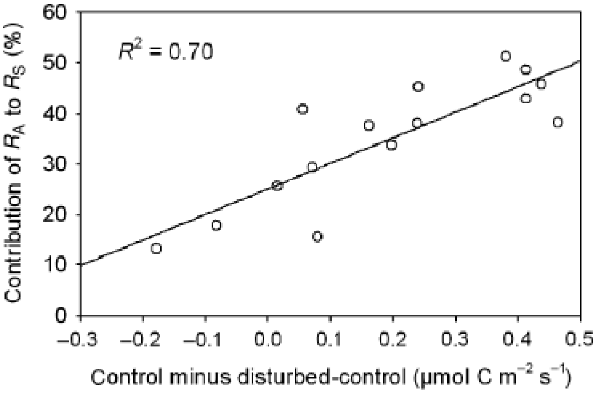

Fig. 5 Differences between control plot CO_2 efflux and disturbed-control plot CO_2 efflux in relation to the amount of (measured) autotrophic contribution to the total soil respiration during 2006.

Discussion

The average ~ 45% increase of R_S during the first two seasons of soil warming was higher than the 20% mean increase found in several ecosystem warming experiments (Rustad *et al.*, 2001) but within observations of other forest soil warming experiments (Peterjohn *et al.*, 1993, 1994; Rustad & Fernandez, 1998; Melillo *et al.*, 2002; Niinistö *et al.*, 2004). The long-term effect of warming is not yet evident from the first 2 years in our experiment. Melillo *et al.* (2002) and Niinistö *et al.* (2004) found the strongest response to warming during the first season and declining effect in the second season. We did not observe a decline so far. Hence, our hypothesis of a strong lasting positive response to the warming on the calcareous site held true for the first two seasons and merits further monitoring.

The annual gaseous C loss from the forest soil of approximately 6.6 t ha^{-1} is within reported values from other temperate sites (e.g. Buchmann, 2000; Borken *et al.*, 2002). The estimated annual aqueous DOC outflow of 0.02–0.03 t ha^{-1} is within the range that has been

Table 1 Seasonally Q_{10} (apparent temperature sensitivity) and R_{10} (CO_2 efflux at 10 °C soil temperature) values derived from mean soil temperatures and mean CO_2 efflux of each measurement date during 2005 and 2006 and Q_{10} values that correspond to the observed response to the + 4 °C soil warming

Treatment	Soil depth (cm)	2005 Q_{10}	2005 R_{10}	2005 R^2	2006 Q_{10}	2006 R_{10}	2006 R^2	+ 4 °C Q_{10}
Warmed (R_S)	5	2.65 (0.50)	2.11 (0.21)	0.92	3.39 (0.58)	2.32 (0.23)	0.94	2.62
	15	2.77 (0.82)	2.26 (0.30)	0.86	3.55 (0.87)	2.68 (0.30)	0.87	
Disturbed control (R_S)	5	3.77 (1.07)	2.20 (0.15)	0.9	3.68 (0,65)	2.35 (0.14)	0.94	
	15	4.01 (1,52)	2.27 (0.17)	0.88	4.33 (1,21)	2.53 (0.17)	0.89	
Control (R_S)	5	4.45 (1.48)	2.48 (0.18)	0.89	4.29 (0.82)	2.59 (0.14)	0.95	
	15	5.11 (2.80)	2.52 (0.24)	0.83	5.02 (1.51)	2.74 (0.19)	0.90	
Trenched-warmed (R_H)	5	2.37 (0.58)	1.37 (0.17)	0.38	3.14 (0.75)	1.55 (0.21)	0.87	2.62
	15	2.54 (1.03)	1.50 (0.23)	0.72	2.85 (1.07)	1.94 (0.30)	0.69	
Trenched-control (R_H)	5	2.70 (0.76)	1.52 (0.09)	0.82	3.24 (0.61)	1.57 (0.10)	0.91	
	15	2.78 (1.13)	1.56 (0.13)	0.76	3.45 (0.91)	1.68 (0.12)	0.87	
Autotrophic (R_A)	5	9.31(8.15)	0.89 (0.18)	0.78	5.25 (1.94)	0.93 (0.11)	0.8	2.92
	15	9.46 (9.45)	0.91 (0.18)	0.76	6.93 (2.45)	1.02 (0.09)	0.87	
Autotr. moist. corr. (R_A)	5	16.7 (26.94)	0.63 (0.24)	0.65	5.32 (2.92)	0.66 (0.16)	0.71	
	15	15.6 (30,80)	0.58 (0.22)	0.60	7.53 (4.49)	0.72 (0.14)	0.79	

Q_{10} values corresponding to the + 4 °C soil warming were derived by fitting Eqn (1) to the mean annual soil temperatures and the mean annual CO_2 effluxes of control and warmed plots. Values in brackets show the 95% confidence intervals.

reported at other forest sites (Michalzik *et al.*, 2003; Fröberg *et al.*, 2005). The C flux in the aqueous phase was almost negligible from a geochemical point of view in comparison with the C export in the gaseous phase.

In our attempt to separate the gaseous C efflux in an autotrophic and heterotrophic component, we had to cope with two problems associated with the trenching technique. Soil moisture was higher on trenched plots because the water uptake of roots was lacking and the decomposition of fine roots on trenched plots was an additional source of heterotrophic CO_2 efflux (Hanson *et al.*, 2000; Ngao *et al.*, 2007). In a companion experiment, we found that fine roots <2 mm accounted for about 2.5 t C ha^{-1} (Díaz-Pinés López de los Mozos *et al.*, in press). Thirty percent of the fine roots were decomposed during the first 15 months after trenching. Presuming a similar development of fine-root decomposition during the first 2 years of soil warming, the additional CO_2 efflux due to fine root decomposition was roughly 0.6 t C yr^{-1}. Applying this estimate and correcting for differences in soil moisture, the contribution of R_A was between 35% and 40% of total R_S during both the growing seasons. The estimate represents the upper end because trenching eliminated potential 'priming' of heterotrophic decomposition due to labile C supply from roots (Subke *et al.*, 2004; Scott-Denton *et al.*, 2006) and probably underestimated R_H.

However, knowledge of the quantitative contribution of R_A to R_S alone does not give all the information that is necessary to quantify the warming effects. The temperature sensitivities of R_A and R_H have to be considered as well. Because of the artifacts of the overheating in 2005 (warmed-trenched plots could have been over-proportionally affected because a part of the labile C likely was 'burned off' and no labile C was supplied by roots), the CO_2 efflux data from 2006 represented a more reliable base to quantify the warming effects R_A and R_H. The almost equal response of the soil CO_2 efflux on warmed (+47%) and trenched-warmed plots (+45%) during 2006 indicated that the temperature sensitivities of R_A, R_S, and R_H were within a narrow range. The estimated response of R_A was slightly stronger (+56%). However, the warming effect on R_A was estimated from deviations between the warming effects on trenched and nontrenched plots. Consequently, it held a much higher uncertainty than the real measured data for R_S and R_H. Hence, the similar effects of soil warming on R_S and R_H make us confident that the temperature sensitivity of R_A was close to that of R_H. This is in line with observations from other field experiments that focused on the soil temperature effect on the fractions of R_S (Bhupinderpal-Singh *et al.*, 2003; Irvine *et al.*, 2005). If the temperature sensitivities of R_A and R_H were similar, and R_A contributed 35–40% to R_S, than roughly 1 t C ha^{-1} yr^{-1} of the overall annual increase in R_S (2.8 t C ha^{-1} yr^{-1}) was autotrophic. This part was mainly fuelled by recent photosynthates from trees. The remaining heterotrophic part (1.8 t C ha^{-1} yr^{-1}) represented the warming induced C loss from SOM.

It has to be considered that R_A consists of different components which were not studied separately in our experiment. The components (e.g. root and mycorrhizal respiration) might have responded differently to the temperature increase. Recent studies have shown that mycorrhizal respiration in forest soils is primarily controlled by substrate supply and to a lesser extent by soil temperature (Heinemeyer *et al.*, 2007; Moyano *et al.*, 2008). Contrary to a microcosm study, where the temperature sensitivity of roots and mycorrhizae was found to be equal (Bååth & Wallander, 2003), no relationship between respiration of mycorrhizal fungi and soil temperature at all was observed in the field (Heinemeyer *et al.*, 2007). Here, we aimed to distinguish between the temperature response of different processes linked to short- and long-term C pools. Because both root and mycorrhizal respiration are primarily fuelled by recent photosynthates, a detailed distinction between the temperature sensitivity of root and mycorrhizal respiration was not essential.

The combination of the soil warming with a trenching experiment brought additional advantages. Throughout the seasons, the difference in CO_2 efflux between the control and the disturbed-control plots was statistically not significantly different. Hence, one would consider that there was no disturbance effect by the cable insertion. However, using the data of the trenching experiment, we found a clear relationship between the difference in control and disturbed-control plot CO_2 efflux and the seasonal development of R_A. A disturbance effect became evident only at times when R_A contributed more than 30% to R_S (Fig. 5). The mere comparison of warmed and control plots would have underestimated the warming effect, whereas the comparison between disturbed-control and warmed plots gave the true warming effect. Collars for CO_2 flux measurements are often inserted at soil depths similar or deeper than our heating cable (3 cm, including the O horizon) (e.g. Borken *et al.*, 2002; Jiang *et al.*, 2005; Khomik *et al.*, 2006). When roots or hyphae are cut by deeply inserted collars, insertion can lead to underestimated CO_2 fluxes, which is especially critical in partitioning studies where the estimate of R_A can become biased (Wang *et al.*, 2005; Heinemeyer *et al.*, 2007).

We observed a distinct seasonal pattern in the development of R_A. The contribution of R_A to R_S was highest during the summer of both seasons (Fig. 4). Similar observations were made by Epron *et al.* (2001) and

Bhupinderpal-Singh *et al.* (2003). This seasonal pattern was even further increased, when we accounted for soil moisture differences between trenched and non-trenched plots. The high contribution of R_A during the warm summer months implied higher seasonal Q_{10} values for R_A compared with R_S and R_H (Table 1). High seasonal Q_{10} values of R_A were found in other trenching experiments as well (Boone *et al.*, 1998; Epron *et al.*, 2001). Transformed into a measure of the temperature sensitivity [Eqn (1)], the high seasonal Q_{10} of R_A suggested that the autotrophic component of the soil respiration was much more temperature sensitive than the heterotrophic component. For a mean temperature increase of 4 °C, the Q_{10} values (9.3 and 5.3) implied a 145% and 95% increase of R_A during 2005 and 2006, respectively. However, the measured increase during soil warming (75% and 56%) was considerably lower. Hence, the seasonally derived Q_{10} values were no indicator for the temperature sensitivity of R_A alone, but reflected other factors as well. It is likely that seasonal variations in photosynthate supply from the canopy to the rhizosphere were reflected in the soil CO_2 efflux (Yuste *et al.*, 2004; Sampson *et al.*, 2007). Gross primary production of a temperate forest typically peaks during summer if soil moisture is not limiting (Falge *et al.*, 2002). Consequently, the high Q_{10} values of R_A likely reflected seasonal variations of various factors such as labile C supply to the roots and rhizosphere, root growth and activity (Epron *et al.*, 2001), as well as soil temperature. Variations in soil moisture were probably not reflected in the high Q_{10} values. Accounting for the differences in soil moisture contents between trenched and control plots even increased the Q_{10} of R_A (Table 1). If the seasonally derived Q_{10} values for R_A did not solely reflect the soil temperature sensitivity, the same applied to R_S in a diminished way. Only the Q_{10} values of R_H represented a more valid measure for the temperature sensitivity of heterotrophic decomposition. Root trenching cut the connections to the canopy and trenched plot soil moisture was constant throughout the seasons. However, beside soil temperature, the Q_{10} of R_H might still have been influenced by seasonal variations in C supply from other sources like leaf litter supply (Gu *et al.*, 2004). Hence, seasonally derived Q_{10} values should be taken with caution or avoided to model temperature effects on soil respiration.

Generally, it has to be noted that we solely warmed the forest soil but not the entire trees. How a warmer atmosphere affects future rates of soil respiration will be at least partly determined by tree physiological responses to increased air temperatures. Higher air temperatures can increase the photosynthetic rate of leaves (Farquhar *et al.*, 1980). Whether or not the amount of labile C that is available for roots increases or decreases depends on different factors such as leaf area development and the development of associated respiration costs (Oren *et al.*, 1986). The availability of substrate and its allocation to aboveground and belowground sinks will determine the rates of the autotrophic soil respiration component. In our warming experiment, R_A was significantly increased. As our plots were rather small and as there were no trees inside the plots, it is likely that the surrounding trees did not fix more C due to the soil warming. Hence, enhanced substrate demand of the roots may have led to an allocation of labile C into the warmed plots. Whether this warming-induced demand on labile C is supplied under warmer air temperatures remains unclear. Experiments that simulate increased air and soil temperatures are still rare and show controversial outcome. Niinistö *et al.* (2004) observed a 27–43% increased soil respiration during 4 years of single tree air/soil warming in a boreal pine forest whereas Bronson *et al.* (2008) found a 23–31% decrease in soil respiration during a combined soil/air warming experiment, but a 24% increase in soil respiration in the soil-only warming treatment in a boreal pine forest. Especially, as manipulation experiments move towards whole ecosystem manipulation with several changing variables such as soil temperature, air temperature, and elevated atmospheric CO_2, it is crucial that emphasis is placed on the understanding of plant and soil interactions. Only an improved understanding of these interactions will reveal whether soil is losing or gaining C under changed climatic conditions.

Conclusions

- Soil warming by 4 °C increased R_S on average by $\sim 45\%$ or $2.8\,\mathrm{t\,C\,ha^{-1}\,yr^{-1}}$ during the first two seasons of soil warming. The warming response was similar during the first and second seasons. Whether this strong response lasts, and for how long it lasts, will be revealed by further monitoring.
- Autotrophic and heterotrophic soil respiration rates responded similarly to soil warming. Between 60% and 65% ($\sim 1.8\,\mathrm{t\,C\,ha^{-1}\,yr^{-1}}$) of the additional CO_2 efflux were heterotrophic. The remaining additional $\sim 1\,\mathrm{t\,C\,ha^{-1}\,yr^{-1}}$ resulted from increased autotrophic soil respiration. It is crucial to quantify the warming effects on the autotrophic and heterotrophic components of R_S. Autotrophic soil processes are tightly coupled to C gain by photosynthesis. Enhanced heterotrophic decomposition of SOM can mean a loss of old, stored C from the soil.
- Q_{10} values for autotrophic soil respiration were very high (5.3–9.3) when derived from the seasonal

development of R_A and soil temperature. The Q_{10} of R_A calculated from the 4 °C warming (2.9) represents the real temperature sensitivity. Hence, seasonally derived Q_{10} values reflected variables other than soil temperature as well and should be avoided to model soil temperature effects on R_A and R_S.

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