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REGULAR ARTICLE

# Experimental forest soil warming: response of autotrophic and heterotrophic soil respiration to a short-term 10°C temperature rise

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**Abstract** We warmed the top soil of a mature coniferous forest stand by means of heating cables on control and trenched plots within 24 h by 10°C at 1 cm soil depth (9°C at 5 cm depth) and measured the effect on the autotrophic ($R_A$) and heterotrophic ($R_H$) component of total soil $CO_2$ efflux ($R_S$). The short time frame of warming enabled us to exclude confounding fluctuations in soil moisture and carbon (C) flow from the canopy. The results of the field study were backed up by a lab soil incubation experiment. During the first 12 h of warming, $R_A$ strongly responded to soil warming; The $Q_{10}$ values were 5.61 and 6.29 for 1 and 5 cm soil depth temperature. The $Q_{10}$ values for $R_A$ were almost twice as high as the $Q_{10}$ values of $R_H$ (3.04 and 3.53). $Q_{10}$ values above 5 are above reasonable plant physiological values for root respiration. We see interactions of roots, mycorrhizae and heterotrophic microbes, combined with fast substrate supply to the rhizosphere as an explanation for the high short-term temperature response of $R_A$. When calculated over the whole duration (24 h) of the field soil-warming experiment, temperature sensitivities of $R_A$ and $R_H$ were similar (no significant difference at $P<0.05$); $Q_{10}$ values were 3.16 and 3.96 for $R_A$ and 2.94 and 3.35 for $R_H$ calculated with soil temperatures at 1 and 5 cm soil depth, respectively. Laboratory incubation showed that different soil moisture contents of trenched and control plots affected rates of $R_H$, but did not affect the temperature sensitivity of $R_H$. We conclude that a single parameter is sufficient to describe the temperature sensitivity of $R_S$ in soil C models which operate on larger temporal and spatial scales. The strong short-term response of $R_A$ may be of relevance in soils suspected to experience increasingly strong diurnal temperature variations.

**Keywords** Autotrophic respiration · Heterotrophic respiration · $Q_{10}$ · Soil respiration · Soil warming

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## Introduction

Soil respiration is the largest terrestrial source of $CO_2$ to the atmosphere and currently represents an annual

flux a magnitude larger than that from anthropogenic fossil fuel combustion (IPCC 2007; Raich et al. 2002). Small climatically induced changes in the rate of soil respiration can have a great impact on future atmospheric $CO_2$ concentrations. In particular, global warming may have the potential to increase $R_S$ and turn terrestrial ecosystems from C sinks to C sources (Cox et al. 2000; Jones et al. 2003). The temperature dependency of the heterotrophic decomposition of different soil C pools is intensively discussed e.g. (Fang et al. 2005; Kirschbaum 2006; Knorr et al. 2005; Reichstein et al. 2005). The temperature sensitivity of $R_A$ remains unclear. $R_A$ consists of root respiration, respiration of their mycorrhizal fungi, and respiration of soil microorganisms closely dependent on recent photosynthates (Högberg and Read 2006). Heterotrophic soil respiration ($R_H$) originates from the decomposition of soil organic matter. In terrestrial ecosystems $R_A$ contributes 10 to 90% to $R_S$, depending on ecosystem and season (Hanson et al. 2000). In forests, roughly half of $R_S$ is autotrophic e.g. (Andersen et al. 2005; Bhupinderpal-Singh et al. 2003; Epron et al. 2001). Different temperature sensitivities of $R_A$ and $R_H$ would affect different soil C pools. $R_A$ utilizes fresh photosynthates (Högberg et al. 2001), while $R_H$ derives from the mineralization of soil organic matter which is stored in large stocks (Batjes 1996). Many C-cycle models use a single factor to describe the temperature sensitivity of $R_S$ (Burke et al. 2003; Tjoelker et al. 2001). Eventual differences in the temperature sensitivities of $R_A$ and $R_H$ may compromise modelling results of future soil C dynamics and atmospheric $CO_2$ concentrations.

In the field, the temperature sensitivity of $R_A$ and $R_H$ is difficult to assess because factors aside from soil temperature simultaneously influence their rates. The calculation of the temperature sensitivity from annual soil respiration measurements can be confounded by seasonal plant physiological dynamics (Bhupinderpal-Singh et al. 2003; Liu et al. 2006; Yuste et al. 2004), soil moisture (Davidson et al. 1998; Lavigne et al. 2004), or by the method of separating autotrophic from heterotrophic soil respiration itself (Kuzyakov 2006). Microcosm experiments are often restricted to seedlings and partly lack the complex plant–root–microorganism interactions established in a forest soil.

In this study, we increased the temperature of a forest soil within a short period of time. We assumed that confounding variables such as C transfer from tree crowns to the rhizosphere, or soil water content were stable within this time frame and that changes in $R_S$, $R_H$, and $R_A$ were driven by soil temperature only. To differentiate the temperature sensitivity of $R_A$ and $R_H$, (1) we warmed the soil of a mature forest on control and trenched plots from 2.0 to 12.1°C at 1 cm soil depth (3.5 to 12.5°C at 5 cm depth) within 24 hours. (2) We performed a lab incubation study with soil samples from the control and trenched plots to check for potential methodological bias.

## Materials and methods

### Site description

The study site is located in the Northern Limestone Alps at 910 m a.s.l. on a north–north–east slope of a mountain in western Austria (47°34′50″N; 11°38′21″E). 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 (FAO 1998). The bedrock is formed of dolomite. Soils have a near neutral pH and a high biological activity (Härtel et al. 2002). O-layer depth did not exceed 2 cm and the depth of the A-horizons varied between 5 and 40 cm depending on the location within the heterogeneous relief. Mean annual air temperature and precipitation were 6.8°C and 1,563 mm, respectively. A detailed description of the site is given in Herman et al. (2002).

### Treatments

In spring 2004, three trenched plots were established, to be able to separate $R_A$ and $R_H$. Trenches around 2.5×5 m plots reached down to solid bedrock. Depth of the trenches was 30 to 80 cm. Root in-growth was inhibited by insertion of a plastic lining. Herbaceous vegetation was repeatedly removed from the trenched plots. The positions of the six control plots were adjacent to that of the trenched plots.

We performed the short-term soil warming experiment from Nov 30th to Dec 1st 2006. Prior to the

experiments, both treatments (trenched, control) were heated by 4°C during the snow free season in 2005 and 2006. Soil was warmed by resistance heating cables (TECUTE – 0.18 Ohm/m/UV, Etherma, Austria), buried 3 cm into the mineral soil. Heating cables were inserted in 2004 on three trenched plots (2×2 m grid) and three control plots (2×2 m grid). Spacing between cables was 7.5 cm. Electricity for the cables was supplied by three heating transformers (primary 230 Vac/50 Hz, secondary 40 V, 79, 2A). A datalogger (CR 10, Campbell Scientific, Inc., North Logan, USA) was used as a control unit.

On Nov 30th 2006 the initial soil temperatures of 2.0°C (1 cm soil depth) and 3.5°C (5 cm depth) were increased to 12.1 and 12.5°C in four steps. The first 3 steps were completed at 4-h intervals. The final step lasted for 12 h as the heating system was close to its power limit and warming proceeded slower.

## Field measurements

Soil temperature was measured during each $CO_2$ measurement at 5 and 1 cm soil depth directly adjacent to the soil respiration chamber using a hand held Thermistor (±0.1°C). Temperature measurements were taken at 5 cm mineral soil depth because most of the roots and organic matter are found in the upper 10 cm of the mineral soil. Temperature measurements at 1 cm soil depth were made to control potential overheating of the top soil layer. Soil moisture at 5 and 15 cm soil depth was measured with $ECH_2O$-10 probes (Decagon, Washington) every 30 min.

At each temperature step, $CO_2$ emissions from control and trenched plots were measured. We further measured the $CO_2$ efflux from three non heated control plots. The chambers for the measurement of the $CO_2$ efflux were round (20 cm diameter, 10 cm height) plastic cylinders, which were placed randomly on the plots and used for replicated $R_S$ measurements in a long-term soil warming study (Schindlbacher et al., manuscript in preparation). Per plot, three measurements were taken using a closed dynamic $CO_2$ measuring system. The chambers were closed with a vented stainless steel lid for 3 min. The chamber headspace $CO_2$ concentration was recorded with an attached portable infrared gas analyzer (EGM 4, PP-Systems, Hitchin UK) every 20 s. $R_S$ was calculated from the linear headspace $CO_2$ concentration increase over the last 2 min.

## Laboratory measurements

About 1 kg soil was sampled randomly from each of the three control and trenched plots. Samples were taken with a soil corer. After removing roots, the soil was sieved (2 mm) and the sub-samples of each plot were pooled. Additionally, four intact soil cores with a known volume were dried at 105°C for 24 h to determine the field bulk density. For each plot, we incubated four replicates (200 $cm^3$ cylinders; field bulk density) at the same temperatures as in the field experiment (5 cm soil depth). $CO_2$ measurements were started at the lowest temperature (3.5°C) and soil temperature was consecutively increased until the highest temperature (12.5°C) was reached. Subsequently, samples were cooled down to the initial temperature and $CO_2$ efflux was re-measured to check for possible substrate loss during incubation.

To analyse the effect of soil moisture on rates of $R_H$, we incubated homogenised soil at different soil moisture levels at a constant soil temperature of 15°C. Initial soil moisture content of the 12 replicates (200 $cm^3$ cylinders; field bulk density) was 56 vol. %. Four replicates were kept at this moisture level during the whole incubation and served as control. Four replicates were watered in 5 vol.% increments and four soil cores were dried in 10 vol.% steps. After watering and during drying, the soil samples were stored at 5°C to avoid too much loss of labile C. Four hours prior to the $CO_2$ measurements, the temperature was shifted to 15°C again. We used the $CO_2$ flux rates from the control samples to correct for decreasing $CO_2$ not related to soil moisture but loss of labile C during the experiment (10 days).

For incubation, we used a fully automated gas measurement system (Schindlbacher et al. 2004). For $CO_2$ measurements, the system was slightly modified. In brief, 12 soil samples were placed in glass chambers. One chamber was empty and acted as reference chamber. The system operated as an open-flow-through method. Ambient air from inside the incubator was sucked through a chamber with a soil sample at 0.5 l $min^{-1}$ to the $CO_2$ analyser. A $CO_2$ reading was taken after the $CO_2$ concentration was stable (after 6 min) using a WMA-4 infrared gas analyzer (PP-

System, Hitchin UK). After each soil chamber, the same procedure was carried out for the empty reference chamber. The $CO_2$ flux was calculated from the soil surface area, air flow rate, and the $CO_2$ concentration difference between the soil chamber and the reference chamber (Schindlbacher et al. 2004). To keep the $CO_2$ concentration in the incubator constant, the incubator was constantly flushed with air at a flow rate of 2.0 l $min^{-1}$.

Total C and dissolved organic carbon (DOC) concentrations of soil samples and microbial biomass were analysed with a Shimadzu-5050 analyser following Schinner et al. (1996). We slightly modified the fumigation-extraction method for microbial biomass C determination by using KCl instead of $K_2SO_4$ extracts (Öhlinger 1996).

### Data analysis

The contribution of autotrophic soil respiration to the total soil respiration was calculated as:

$$R_A = R_S - R_H \quad (1)$$

Where $R_A$ is the autotrophic soil respiration, $R_S$ is the $CO_2$ efflux from the control plots and $R_H$ is the $CO_2$ efflux from the trenched plots. $CO_2$ efflux from the root-free soil samples which were incubated in the lab was attributed to $R_H$ only.

The temperature response of $R_S$, $R_H$, and $R_A$ was estimated by means of a $Q_{10}$ function (Janssens and Pilegaard 2003):

$$R = R_{10} * Q_{10}^{((T-10)/10)} \quad (2)$$

In which $R$, the dependent variable, is the measured soil $CO_2$ efflux, $R_{10}$ is the simulated soil respiration at 10°C, $Q_{10}$ is 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 non-linear least square fitter (SigmaPlot for Windows, Version 10, SyStat Software, Inc.). $Q_{10}$ values were calculated for each plot because the soil temperatures of the different plots were not precisely uniform during the field measurements and the in-situ warming experiment. Mean $Q_{10}$ of $R_S$, $R_H$ and $R_A$ were statistically analysed using a one way ANOVA (SAS Institute, Inc., Cary, NC, USA). Group means were compared with a Duncan's test (Duncan 1955).

## Results and discussion

During the field soil warming experiment, soil temperatures increased simultaneously on trenched and control plots. Soil temperatures at 1 and 5 cm soil depth showed similar trend but the initial soil temperature was 1°C lower at 1 cm soil depth (Fig. 1a,b).

$CO_2$ fluxes from all plots increased with increasing soil temperature (Fig. 1c). The response of $R_A$ within the first 12 h of warming was explicitly strong. $Q_{10}$ values of $R_A$ exceeded $Q_{10}$ values of $R_H$ by factor of ~2 (Table 1). When calculated over the entire duration of the experiment $Q_{10}$ values of $R_A$, $R_H$, and

**Table 1** $Q_{10}$ values (±SE, $n$=3) as a measure for temperature sensitivities of $R_S$ (Control), $R_H$ (Trench), $R_A$ (Autotrophic), and $Q_{10}$ for $R_A$ adjusted by the relative difference between $R_H$ rates from trenched and control soil during the lab incubation (Autotr. adjusted)

| Data source | Soil depth | Temp. Range | Control | | Trench | | Autotrophic | | Autotr. adjusted | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | $Q_{10}$ | $R^2$ | $Q_{10}$ | $R^2$ | $Q_{10}$ | $R^2$ | $Q_{10}$ | $R^2$ |
| Soil warming | | | | | | | | | | |
| 0–12 h | 1 | 2.0–10.5 | 3.32[a] (0.23) | 0.95 | 3.04[a] (0.16) | 0.95 | 5.61[a] (1.82) | 0.63 | 8.27[a] (4.38) | 0.56 |
| | 5 | 3.5–10.7 | 3.67[a] (0.12) | 0.97 | 3.53[a] (0.19) | 0.86 | 6.29[b] (0.54) | 0.78 | 12.64[b] (3.15) | 0.68 |
| 0–24 h | 1 | 2.0–12.1 | 2.82[a] (0.41) | 0.94 | 2.94[a] (0.06) | 0.96 | 3.16[a] (0.54) | 0.62 | 3.51[a] (1.09) | 0.35 |
| | 5 | 3.5–12.5 | 3.14[a] (0.40) | 0.96 | 3.35[a] (0.20) | 0.89 | 3.96[a] (0.83) | 0.70 | 5.13[a] (1.89) | 0.44 |
| Lab – incubation | 0–10 | 3.5–12.5 | 2.47[a] (0.12) | 0.96 | 2.33[a] (0.36) | 0.86 | | | | |

$Q_{10}$ values were calculated over different temperature/time ranges and for soil temperatures at 1 and 5 cm mineral soil depth. $Q_{10}$ from the laboratory incubation from both, control and trenched plots were obtained from root free samples and reflect $R_H$ only. Significantly differences between mean $Q_{10}$ ($P$<0.05) are indicated by different letters

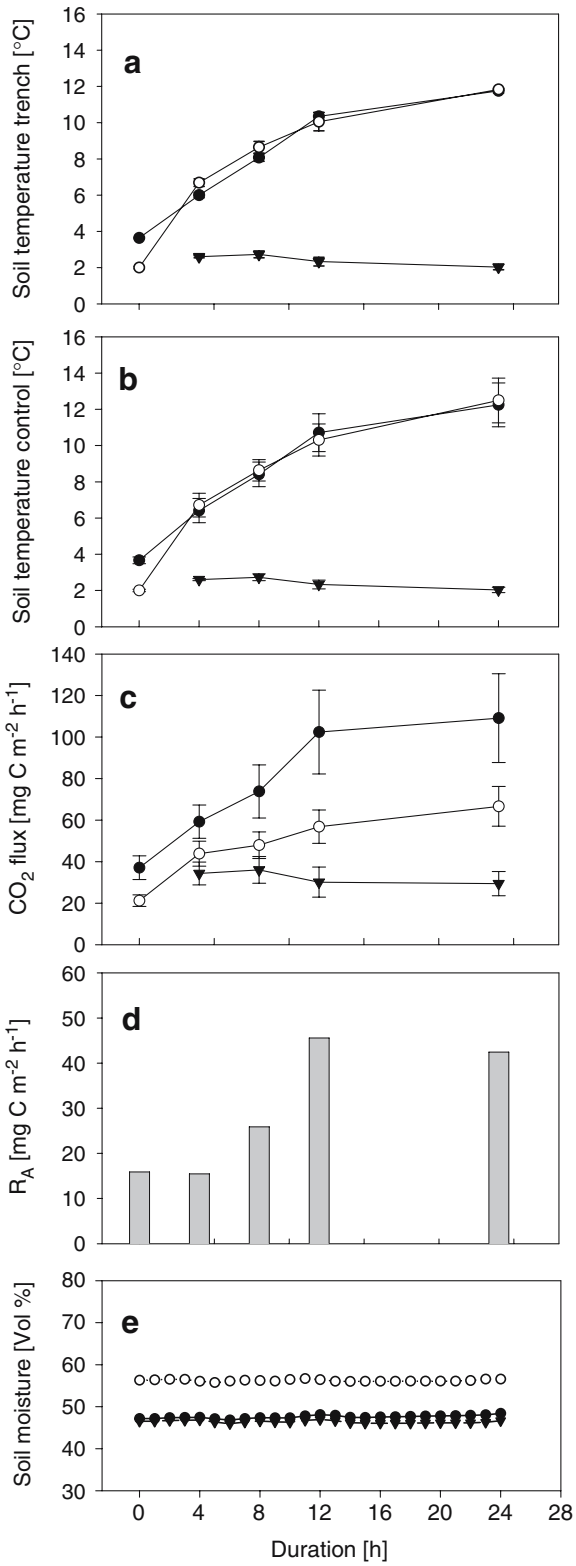


**Fig. 1** Development of soil temperature, moisture and $CO_2$ efflux during the field soil warming. **a** Soil temperature (±SE; $n$=3) on trenched plots at 1 cm depth (*open circles*), 5 cm depth (*filled circles*) and on untreated control plots (*triangles*). **b** Soil temperature on heated control plots and on untreated control plots (same indication than **a**). **c** Mean $CO_2$ efflux (±SE; $n$=3) from the trenched plots ($R_H$, *open circles*), heated control plots ($R_S$, *filled circles*), and untreated control plots (*triangles*). **d**: Development of $R_A$ as computed by equation (1), **e**: Soil moisture at 5 cm soil depth on trenched plots (*open circles*), heated control plots (*filled circles*) and non heated control plots (*triangles*)

$R_S$ were not statistically significantly different. However, the $CO_2$ efflux over time was different. $CO_2$ efflux from control plots ($R_S$) increased strongly during the first 12 h. Afterwards only a slight response of $R_S$ to the increasing soil temperature was observed (Fig. 1c). $CO_2$ efflux from trenched plots ($R_H$) increased more uniformly during the experiment. Applying Eq. 1, $R_A$ strongly increased during the first 12 h and then decreased slightly during the last 12 h of warming (Fig. 1a).

Soil moisture content did not change throughout the warming but was 9 vol.% higher on trenched plots than on control plots. Higher soil moisture contents compared to the control is a known problem in trenching experiments because the water uptake of roots is lacking on the trenched plots (Hanson et al. 2000). Because soil moisture probably influences the temperature sensitivity of $R_H$ (Gaumont-Guay et al. 2006; Janssens and Pilegaard 2003; Wang et al.

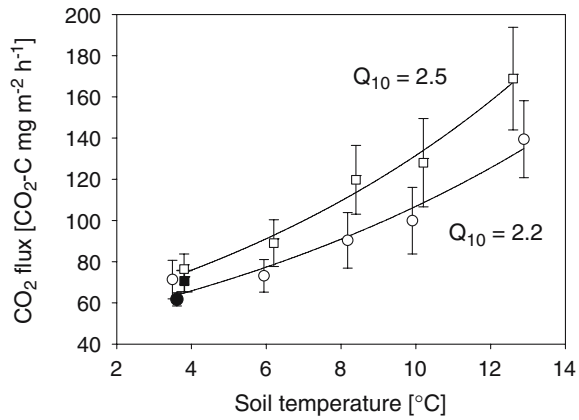


**Fig. 2** $CO_2$ fluxes (±SE; $n$=4) from soil of trenched plots (*circles*) and control plots (*squares*) incubated in the laboratory. Soil temperature was increased consecutively during the incubation. After reaching the highest temperature, soil was cooled to the initial temperature of 3.5°C and $CO_2$ flux was re-measured (*filled symbols*). The differences between the full and *open symbols* indicate the substrate loss during the 3 days of incubation

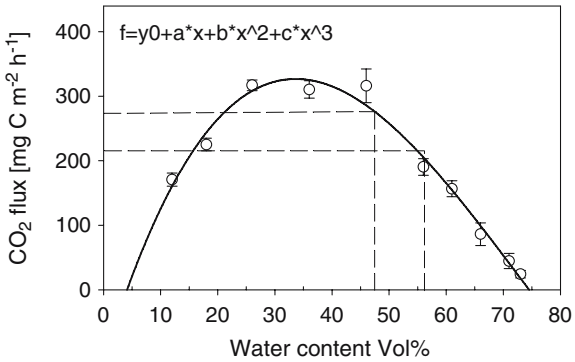


**Fig. 3** $CO_2$ efflux (±SE; $n$=4) of incubated, homogenised soil under different soil moisture contents. *Dashed lines* indicate the different soil moisture contents between trenched and control plots during the field measurements

2006), we incubated root free soil samples from trenched and control plots in the lab at the same water contents. $Q_{10}$ values for $R_H$ in the lab were lower than in the field and no statistically significant differences between control and trenched plots were found (Table 1). Hence different soil moisture contents should not have affected the temperature sensitivity of $R_H$ in the field. The lower $Q_{10}$ values in the lab experiment were most likely caused by substrate loss during the incubation (Reichstein et al. 2000). $CO_2$ flux, re-measured at the initial soil temperature after the 3 days of incubation was lower than the initial $CO_2$ flux (Fig. 2). Substrate loss during incubation should have primarily occurred at higher soil temperatures and thereby lowered the temperature response curve.

Despite similar temperature sensitivity, rates of $R_H$ differed in the lab experiment. $R_H$ from control plot soil was on average 17% higher than $R_H$ from trenched plots. Figure 3 shows a likely explanation for lower $R_H$ rates from trenched plots. $R_H$ from incubated soils decreased sharply under wet and dry conditions. During the short-term warming experiment, soil moisture of the trenched plots was beyond the optimal range for soil respiration (Figs. 1e and 3). This could explain lower rates of $R_H$ from soil samples of the trenched plots. Another reason for lower rates of $R_H$ from trenched plots soil could be depletion of labile C. Since trenched plots did not receive labile C from roots for more than 2 years, they might have become depleted of labile C compared to the control plots. However, DOC values from both treatments were similar and do not indicate a substantial loss of labile C from the trenched plots so far.

Underestimated $R_H$ from trenched plots in the field would imply overestimated rates of $R_A$. This could also have affect $Q_{10}$ values of $R_A$. To correct a potentially overestimated $R_A$, we increased the field $R_H$ values by the mean difference between $R_H$ from trenched and control plots in the lab (17%) and calculated adjusted $Q_{10}$ values for $R_A$. When corrected, mean $R_A$ decreased from 38 to 28% of total $R_S$. Adjusted $Q_{10}$ values were higher but showed the same trend with high temperature sensitivity during the first 12 h of warming and equally temperature sensitivity compared to $R_H$ over the whole 24 h of warming (Table 1). However, adjusted $Q_{10}$ values were less confident than the $Q_{10}$ values calculated from original field data. Differences between $R_S$ and $R_H$ became smaller and non temperature-related heterogeneity in $CO_2$ fluxes from different plots became more evident and was reflected in low $R^2$ of fitted $R_A$ data and high variability of the $Q_{10}$ values (Table 1).

The high temperature sensitivity of $R_A$ during the first 12 h of the field warming resulted in $Q_{10}$ values above reasonable physiological values for root respiration (Pregitzer et al. 2000). Confounding fluctuations in C transfer from the canopy to the rhizosphere can be excluded because $R_S$ from untreated control plots constantly decreased with decreasing soil temperature (Fig. 1b,c). Fluctuations in C flow from the canopy would have been visible in the $CO_2$ flux from the untreated control plots. In contrast to Högberg and Högberg (2002), who observed lower DOC concentrations on girdled plots, bulk soil DOC concentrations and microbial biomass C were similar on control and trenched plots in our study (Table 2). Because

**Table 2** Total C, DOC, and microbial C concentrations of mineral soil samples (0–5 cm soil depth) (±SE, $n$=3) from control and trenched plots

| Plot | C – total (%) | DOC – $H_2O$ (mg/l) | DOC – KCl (mg/l) | Biomass-C–KCl (mg/l) |
|---|---|---|---|---|
| Untreated control | 13.05 (0.20) | 26.94 (1.65) | 9.03 (0.80) | 255.13 (13.42) |
| Control | 14.17 (2.71) | 26.34 (3.10) | 10.91 (0.95) | 227.76 (58.79) |
| Trenched | 15.16 (1.93) | 30.54 (3.89) | 13.23 (2.76) | 237.65 (32.99) |

the temperature sensitivity of soil respiration tends to be highest when substrate is least limiting (Davidson and Janssens 2006; Davidson et al. 2005), the strong temperature response of $R_A$ during the first 12 h could be associated with higher/faster substrate supply in the rhizosphere. We were not able to measure changes in labile rhizosphere C during the field warming experiment. However, labile soil C concentrations are generally higher in the rhizosphere (Cheng et al. 1996). Tree roots are rich in starch and sugars during autumn (Kozlowski and Pallardy 1997) and active transport of sugars in roots and mycorrhiza is faster than passive diffusion of labile C in bulk soil (Tlalka et al. 2002). An initial release of stored C from roots combined with high activity of mycorrhiza, associated microbes, and possibly heterotrophic microbes due to priming effects (Bader and Cheng 2007), would be a potential reason for the strong response of $R_A$ during the first 12 h of soil warming. The slight decrease of $R_A$ during the last 12 h of warming might be caused by decreasing substrate supply. Another explanation would be the physiological acclimation of root respiration to the increased temperatures, even if less likely during the short period (Atkin et al. 2000; Burton and Pregitzer 2003; Loveys et al. 2003).

Despite the strong initial response of $R_A$, temperature sensitivities of $R_A$, $R_S$ and $R_H$ were similar over the whole 24 h of warming (Table 1). This is in contrast to Boone et al. (1998), who used the same technique to separate $R_A$ from $R_H$ but reported a significantly higher temperature sensitivity of $R_A$. However, they calculated $Q_{10}$ values from a time series of soil respiration measurements during an entire season which may reflect changes of other environmental and plant physiological variables as well. Like in our study, similar temperature sensitivity of $R_A$ and $R_H$ was observed in studies which were particularly designed to overcome confounding influences from other factors than soil temperature (Bååth and Wallander 2003; Bhupinderpal-Singh et al. 2003; Irvine et al. 2005). Closest to our approach, Bååth and Wallander (2003) measured $CO_2$ efflux from microcosms, where root, mycorrhizal, and bulk soil respiration were separated. Compared to our study, they obtained lower (2.2–2.4), but similar $Q_{10}$ values for the three compartments. However, soil temperature was shifted from 5 to 15°C in one step and the $CO_2$ efflux was detected as mean flux over 3 days. Hence, short-term response to increasing soil temperature was not detected, but might have differed between autotrophic and heterotrophic soil respiration in their experiment as well.

We conclude that a single model parameter is sufficient to describe the temperature sensitivity of $R_S$ in soil C models which operate on larger temporal and spatial scales. The strong initial response of $R_A$ to increased soil temperature may be of relevance in forests susceptible to increasingly strong diurnal temperature variations.

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