Does the temperature sensitivity of decomposition of soil organic matter depend upon water content, soil horizon, or incubation time?

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Abstract
Several studies have shown multiple confounding factors influencing soil respiration in the field, which often hampers a correct separation and interpretation of the different environmental effects on respiration. Here, we present a controlled laboratory experiment on undisturbed organic and mineral soil cores separating the effects of temperature, drying–rewetting and decomposition dynamics on soil respiration. Specifically, we address the following questions:
(1) Is the temperature sensitivity of soil respiration ($Q_{10}$) dependent on soil moisture or soil organic matter age (incubation time) and does it differ for organic and mineral soil as suggested by recent field studies.
(2) How much do organic and mineral soil layers contribute to total soil respiration?
(3) Is there potential to improve soil flux models of soil introducing a multilayer source model for soil respiration?

Eight organic soil and eight mineral soil cores were taken from a Norway spruce ($Picea abies$) stand in southern Germany, and incubated for 90 days in a climate chamber with a diurnal temperature regime between 7 and 23 °C. Half of the samples were rewetted daily, while the other half were left to dry and rewetted thereafter. Soil respiration was measured with a continuously operating open dynamic soil respiration chamber system. The $Q_{10}$ was stable at around 2.7, independent of soil horizon and incubation time, decreasing only slightly when the soil dried. We suggest that recent findings of the $Q_{10}$ dependency on several factors are emergent properties at the ecosystem level, that should be analysed further e.g. with regard to rhizosphere effects. Most of the soil CO$_2$ efflux was released from the organic samples. Initially, it averaged 4.0 μmol m$^{-2}$ s$^{-1}$ and declined to 1.8 μmol m$^{-2}$ s$^{-1}$ at the end of the experiment. In terms of the third question, we show that models using only one temperature as predictor of soil respiration fail to explain more than 80% of the diurnal variability, are biased with a hysteresis effect, and slightly underestimate the temperature sensitivity of respiration. In contrast, consistently more than 95% of the diurnal variability is explained by a dual-source model, with one CO$_2$ source related to the surface temperature and another CO$_2$ source related to the central temperature, highlighting the role of soil surface processes for ecosystem carbon balances.

Keywords: drying–rewetting, dual-source model, incubation experiment, $Q_{10}$, soil moisture, soil respiration

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Introduction

Considering that terrestrial ecosystems take up about one-third of the CO₂ emissions from anthropogenic fossil fuel burning and cement manufacturing (Schimel et al., 2001), it is critical to improve our knowledge and understanding of the carbon exchange between terrestrial ecosystems and the atmosphere. At 68–80 Pg C yr⁻¹, soil respiration represents the second largest global carbon flux between ecosystems and the atmosphere (Raich & Schlesinger, 1992; Raich & Potter, 1995; Raich et al., 2002). This amount is more than 10 times the current rate of fossil fuel combustion and indicates that each year around 10% of the atmosphere’s CO₂ cycles through the soil. Thus, even a small change in soil respiration could significantly intensify – or mitigate – current atmospheric increases of CO₂, with potential feedbacks to climate change. Despite this global significance as well as considerable scientific commitment to its study over the last decades, there is still only limited understanding of the factors controlling temporal and interecosystem variability of soil respiration.

It is clear that the most important factors influencing soil respiration are soil temperature, soil water availability, and substrate quality and availability, the latter being influenced by supply strength through vegetation (photosynthate transport, root growth and exudation). There are, however, ambiguous results showing the extent to which soil respiration factors interact. This lack of understanding partly stems from the fact that many studies were performed under uncontrolled field conditions where several co-varying factors are difficult to isolate. Controlled laboratory experiments, on the other hand, have often been performed on disturbed soil samples (mixed and/or sieved, roots removed), substantially altering the environment such that a transfer of results to the ecosystem level seems dubious (e.g. Winkler et al., 1996; Lomander et al., 1998; Reichstein et al., 2000). Moreover, soils are often incubated at different and constant temperatures, which introduces the confounding effect that with time substrate availability (and potentially microbial community) changes among samples, as labile pool sizes decline more rapidly in the higher temperature treatment (see Reichstein et al., 2000 for a detailed discussion). For example, Fang & Moncrieff (2001) form an exception in that they tested the temperature dependence on undisturbed soil samples, and exposed all samples to identical temperature regimes. However, their investigation into interdependencies with soil moisture only considered broad moisture classes with ‘relatively dry’ as the driest of three categories, and accordingly no moisture effects were found.

In the context of global warming, it is particularly important to understand the temperature sensitivity of soil respiration, as it is anticipated that in a warmer world ecosystems provide a positive feedback to the greenhouse effect because of the stronger response of respiratory processes to temperature, compared with assimilatory processes, which are easily limited by light and nutrient supply (e.g. Kirschbaum, 2000). Recently developed coupled climate-vegetation models predict that the current biospheric CO₂ sink will cease during this century, partly because of enhanced respiration in a warmer climate (Cox et al., 2000), assuming an exponential relationship between temperature and respiratory processes with a doubling per 10°C ($Q_{10}$ relationship). On the contrary, a number of field studies at varying scales have cast some doubt on the correctness of such an invariable $Q_{10}$ relationship. For instance, Giardina & Ryan (2000) did not find a clear trend of turnover rates with mean annual temperature, Liski et al. (1999) observed decomposition rates of old organic matter to be temperature insensitive, and a number of studies found a varying temperature sensitivity of soil and ecosystem respiration ($Q_{10}$ between 1 and 4), depending on the soil water availability (e.g. Carlyle & Ba Than, 1988; Xu & Qi, 2001; Reichstein et al., 2002, 2003).

To better understand this critical issue, we continuously observed CO₂ efflux in a controlled experiment from minimally disturbed forest soil monoliths. We specifically addressed the following questions concerning the temperature sensitivity of soil respiration. (1) Is the temperature sensitivity of soil respiration ($Q_{10}$) dependent on soil moisture, drying/rewetting events, or soil organic matter (SOM) age? (2) How much do organic and mineral soil layers contribute to total soil respiration and do their temperature sensitivities differ? (3) How do estimates of the temperature sensitivity change when fluxes from two layers are accounted for compared with single-layer models?

Materials and methods

Soil sampling

Intact soil monoliths, each from the organic and the upper mineral horizon, were sampled randomly in a mature spruce forest (‘Weidenbrunnen’, Picea abies; 114 years old) in the Fichtelgebirge, a small mountain range in SE Germany in April 2001. The local soil type is a cambic podzol over granitic bedrock with low pH values in the mineral (2.9–4.5) and organic (2.6–3.6) layers. The average depth of the organic layer (including surface litter) was $11 \pm 1$ cm, and forest ground vegetation at the sampling locations was dominated by...
the two grass species *Deschampsia flexuosa* and *Calamagrostis villosa*. The main properties of the soil horizons are described in Table 1. Field measurements of soil CO₂ efflux have been carried out during the growing season in 1999. A more complete site description, as well as, analytical results and flux observations are reported in Subke et al. (2003).

The sampling took place 2 days after a period of considerable rainfall, implying that the soils were near field capacity. Cylindrical soil cores were taken of the organic layer using a custom built steel cutter of 30 cm diameter. After inserting the cutter between 15 and 20 cm into the forest floor, the monolith was carefully retrieved from the cutter (having removed remaining mineral soil from the base of the sample), and transferred to custom-built polyvinyl chloride (PVC) containers. Mineral soil samples were taken after removing the organic horizons by inserting the cutter into the mineral soil to a similar depth to the organic soil samples in close proximity to the location where the organic layer sample was taken. The strong build of the cutter allowed it to be forced into the soil using a sledgehammer. It was, therefore, readily possible to cut through roots of up to approximately 2 cm in diameter, while sampling attempts were aborted if larger roots were encountered, as it would have resulted in considerable sample disturbance to force the cutter under these conditions. Mean sample volumes of both mineral and organic soil were 8.1 ± 1.6 dm³ with no significant difference between mean volumes of the two soil layers. The properties of the soil samples harvested after the incubation are shown in Table 1.

The cylindrical sample containers were built from large PVC pipes (30 cm diameter, 1 cm wall thickness), and measured 25 cm in height (Fig. 1a). The base of the containers was formed by a 1 cm PVC disk, which was perforated with about 20 holes of 1 cm diameter allowing excess water to drain during the course of

### Table 1 Description of the soil profile and the soil samples

<table>
<thead>
<tr>
<th>Object</th>
<th>Thickness (cm)</th>
<th>Total organic C (g kg⁻¹)</th>
<th>C/N ratio (g g⁻¹)</th>
<th>Texture (sand/silt/clay)</th>
<th>Bulk density (g cm⁻³)</th>
<th>pH (CaCl₂)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Soil horizons</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>1</td>
<td>478</td>
<td>24.8</td>
<td>nd</td>
<td>nd</td>
<td>3.6</td>
</tr>
<tr>
<td>Of</td>
<td>5</td>
<td>372</td>
<td>20.7</td>
<td>nd</td>
<td>nd</td>
<td>2.9</td>
</tr>
<tr>
<td>Oh</td>
<td>7</td>
<td>376</td>
<td>22.6</td>
<td>nd</td>
<td>nd</td>
<td>2.9</td>
</tr>
<tr>
<td>Ahe</td>
<td>10</td>
<td>38.9</td>
<td>22.9</td>
<td>52/38/10</td>
<td>0.97</td>
<td>3.3</td>
</tr>
<tr>
<td>Bh</td>
<td>2</td>
<td>90.5</td>
<td>22.6</td>
<td>34/50/16</td>
<td>nd</td>
<td>3.9</td>
</tr>
<tr>
<td>Bhs</td>
<td>18</td>
<td>53.6</td>
<td>14.1</td>
<td>45/45/10</td>
<td>0.73</td>
<td>4.3</td>
</tr>
<tr>
<td>Bv-Cv</td>
<td>25</td>
<td>8.4</td>
<td>16.8</td>
<td>46/43/11</td>
<td>1.36</td>
<td></td>
</tr>
<tr>
<td><strong>Incubated samples</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Organic</td>
<td>0–2 cm</td>
<td>2</td>
<td>488 (34)</td>
<td>27.7</td>
<td>nd</td>
<td>0.11 (0.02)</td>
</tr>
<tr>
<td></td>
<td>2–6 cm</td>
<td>4</td>
<td>381 (23)</td>
<td>22.3</td>
<td>nd</td>
<td>0.41 (0.12)</td>
</tr>
<tr>
<td></td>
<td>6–12 cm</td>
<td>6</td>
<td>371 (21)</td>
<td>21.7</td>
<td>nd</td>
<td>0.52 (0.11)</td>
</tr>
<tr>
<td></td>
<td>Mineral</td>
<td>12</td>
<td>45.2 (4.2)</td>
<td>22.6</td>
<td>nd</td>
<td>0.92 (0.21)</td>
</tr>
</tbody>
</table>

Values in parentheses represent one standard deviation (n = 8).

*(Subke et al., 2004a), (Kalbitz, 2004, neighbouring stand with same soil type).

This study.

nd, not determined.
the experiment, preventing water logging. The perforated base was covered with 1 mm mesh nylon gauze to contain soil samples. The container base was raised by approximately 3 cm above the lower end of the cylinder to provide drainage space for excess water, and containers were placed in PVC saucers in the lab to create a gas seal.

Laboratory set-up, soil moisture and temperature treatments

After about 4 h of sampling in the field, the soil cores were immediately taken to a climate chamber (1.5 h transport). The eight samples of each layer were randomly split into two different water treatments, one with a constant moisture treatment and one with a drying–rewetting treatment, resulting in four types of soil cores with four replicates each: Organic soil/constant moisture (OC), organic soil/dry (OD), mineral soil/constant moisture (MC), and mineral soil, dry (MD). For conciseness, the ‘constant moisture’ and the ‘drying–rewetting’ treatment are called wet and dry treatment, respectively. The samples were set up within the climate chamber in a randomized design to eliminate possible (undetected) gradients in temperature or air circulation within the chamber. Above-ground plant parts of the ground vegetation were removed at the beginning of the experiment, as was any regrowth during the course of the experiment.

All soil samples were weighed upon arrival in the lab, and the recorded mass was considered as reference conditions for soil moisture, under which no limitations of soil CO₂ production exist. Over an initial period of 10 days, the mass of all monoliths was recorded daily. Based on the loss of mass in 24 h, water was added to each of the samples in the wet treatments by spraying the given amount of water onto the surface of each sample. After this initial period of 10 days, the wet treatments were sprayed with water every day according to the average loss previously experienced and the mass of all containers was controlled every 3–4 days. The samples of the dry treatments were watered to initial water status within 24 h towards the end of the experiment (OD samples on day 76, MD samples on day 86). At the end of the experiment, the dry weight and the volume of the samples was determined, so that volumetric soil moisture could be calculated from the recorded masses. To allow for comparison between the different soil horizons, these water contents were converted into soil water matric potential using Van Genuchten parameters (Van Genuchten, 1980). The parameters were optimized to describe the observed field capacity and permanent wilting point of the retention curve well and were previously used successfully to model the soil water dynamics at the site (Subke et al., 2003).

Air temperature within the climate chamber cycled between 7 and 23 °C every day, while the dew point within each chamber was kept constant at 4 °C. Following a ‘cold’ period, the temperature was set to 23 °C for 6 h, before moderation to 20 °C for another 6 h. Similarly, temperatures were reduced drastically to 7 °C following the warm period, before moderation to 10 °C.

As one part of this study involved the analysis of the soil respiration dynamics in relation to vertical temperature gradients (with the dual-source model) we executed a prior experiment to understand if the temperature conduction in our set up was mainly in the vertical direction as in field conditions. Here, we installed each five temperature sensors 2 cm below the surface, at the centre and 2 cm above the bottom of the soil core in a radial symmetric manner in the form of a cross (each one sensor at the center and four sensors at 2 cm from the container wall). This prior experiment showed that radial temperature gradients were negligible, an order of magnitude lower than vertical gradients (Fig. 2). We explain this quasiradial insulation of the soil core as a combination of an insulation effect of the containers, and much stronger convective heat transport at the surface of the core because of continually circulating air in the headspace of the open dynamic chamber and a self-insulation effect, as the containers were placed densely next to each other. The results show further that changes in temperature are attenuated within the first few centimetres of a monolith. Therefore, we regard the central temperature as a reasonable approximation of the bulk monolith temperature, while the temperature of the surface layer.
is best described by direct measurements. For the CO₂ efflux experiments, temperature probes were hence installed at the centre of each of the soil monoliths, and each of the five chamber lids used for soil CO₂ efflux also carried a temperature probe that made contact with the soil surface of the monolith where efflux measurements were conducted.

**CO₂ efflux measurements**

A soil CO₂ efflux system designed for continuous measurements from soil chambers in the field (Subke et al., 2003) was used to monitor CO₂ evolution from the monoliths. A simple PVC collar allowed the field chamber lids to fit onto the monolith container ensuring air-tight seals at all connecting points (Fig. 1). The measuring system allows sequential CO₂ flux measurements from five collars and an additional intake for zero calibration, with sampling intervals set to 5 min between collars, so that two readings were obtained per collar per hour. The lids were moved between soil containers every day at about the same time (between 13:00 and 14:00 hours), in a way that at any time, each soil treatment was included in the measuring cycle. Upon restoring the initial water status of the samples in the dry treatments, the allocation of lids was altered with four lids monitoring only rewatered samples, for 10 days, while one lid continued to rotate between other treatments.

**Field measurements**

Parallel to the lab incubation (May–June), we measured soil CO₂ efflux in the field at the same forest stand where soil samples had been taken. The field set-up was the same as described in detail for measurements in 1999 in the same forest stand (Subke et al., 2003). Briefly, 15 soil collars were installed in five groups of three collars. These five groups were located within the same part of the forest stand where samples had been taken, but a minimum distance of 2 m was kept between sampling sites and collar locations. Soil CO₂ efflux was measured sequentially from one of five chamber lids which were placed on one collar in each group, forming an open dynamic soil CO₂ efflux chamber. The automated set-up produced hourly efflux measurements from each of the lids. Lids were moved between collars in each group every 2–3 days to prevent measuring artefacts from prolonged measuring periods. Hourly averages of measurements from all collars were used to estimate the spatial mean of the stand soil CO₂ efflux.

**Data analysis**

Each diurnal cycle of soil CO₂ efflux was analysed by two different models relating CO₂ efflux to soil temperature. Model I was the commonly applied approach where soil respiration is modelled as a function of soil temperature at a certain location in the soil:

\[
R_{\text{soil}} = R_{\text{ref}} Q_{10}^{(T_{\text{soil}}-T_{\text{ref}})/10\, ^{\circ}C}.
\]  

(1)

\(R_{\text{soil}}\) is the instantaneous soil CO₂ efflux (µmol m⁻² s⁻¹), \(T_{\text{soil}}\) is the soil temperature (°C) at the centre of the soil core, \(R_{\text{ref}}\) is the reference efflux (µmol m⁻² s⁻¹) at \(T_{\text{ref}} = 15\, ^{\circ}C\), and \(Q_{10}\) the parameter that determines the temperature response of the soil CO₂ efflux (i.e. the factor by which efflux increases for an increase in temperature by 10 °C). We also analysed the data with the model by Lloyd & Taylor (1994), but results were indistinguishable within the temperature range of this study, in agreement with (Kätterer et al., 1998). The Lloyd-and-Taylor and the \(Q_{10}\) models only differ substantially, when larger temperature ranges are considered. We present here the results from the \(Q_{10}\) model for the intuitiveness of the \(Q_{10}\) parameter and because a majority of ecosystem models are (still) using this function (cf. reviews by Rodrigo et al., 1997; Cramer et al., 2001). For a given temperature, the \(Q_{10}\) and \(E_{0}\) (the temperature sensitivity parameter of the Lloyd-and-Taylor model) can be converted into each other (see Reichstein et al. (2003) for details).

While still very simplified, model II partly accounts for the fact that the soil temperature distribution cannot be represented by a single temperature measurement. It is assumed that the total soil respiration can be attributed to two major sources, a surface layer and the bulk soil (Fig. 2), expressed as:

\[
R_{\text{soil}} = R_{\text{surf.ref}} Q_{10}^{(T_{\text{surf}}-T_{\text{ref}})/10\, ^{\circ}C} + R_{\text{cent.ref}} Q_{10}^{(T_{\text{cent}}-T_{\text{ref}})/10\, ^{\circ}C},
\]  

(2)

where symbols are as in the previous equation, but the subscripts ‘surf’ and ‘cent’ mean ‘of the surface compartment’ and ‘of the bulk soil compartment’, characterized by the temperature at the soil surface and at the centre of soil core, respectively. For clarity, \(T_{\text{cent}}\) in model II and \(T_{\text{soil}}\) in model I, are physically the same; we only differentiate for conceptual reasons.

Mathematically, model II represents a rough discretization of the volume integral

\[
R_{\text{soil}}(t) = \frac{1}{A} \int \int \int R(x, y, z, t) \, dx \, dy \, dz,
\]  

(3)

where \(R(x, y, z, t)\) is the respiration density (per volume; µmol m⁻³ s⁻¹) at the specified location and time, and \(A\) is the area over which the flux is observed, neglecting physicochemical processes (diffusion, solution, etc.).
Apart from the discretization another simplification of the model formulation is that the $Q_{10}$ is assumed to be the same in both soil compartments. This model described the data equally as well as more complex formulations (e.g. with different $Q_{10}$ by compartment, and/or more layers), which were found to be over-parameterized (high parameter correlations, unidentifiable parameters). In the following, models I and II will be referred to as ‘single-source’ and ‘dual-source’ models, respectively.

The model parameters were estimated by a common nonlinear regression algorithm using the least-sum-of-residual-squares criterion (Levenberg–Marquardt algorithm, implemented in the PV-WAVE 7.0 advantage package, function nlinlsq, Visual Numerics Inc., 2001). Standard errors of parameter estimates were calculated according to Draper & Smith (1981), using standard assumptions (e.g. normality and independence of the residuals).

Results

Soil temperature and moisture

While the surface temperature responded fastest to changes in air temperature, the temperature at the centre of a sample never reached the value of the air temperature, even at the end of respective ‘cold’ and ‘warm’ periods (Fig. 3). Soil water availability decreased in all samples of the dry treatment, as is shown by the decrease in matric potential throughout the experiment (Fig. 4). As water was primarily lost via passive evaporation (no water extraction by transpiration) the samples did not dry down near the permanent wilting point but rather to matric potentials around $-1000$ to $-2000$ hPa, even after 80 days in relatively dry air (dew point $4\,^{\circ}\text{C}$).

Soil CO$_2$ efflux in relation to temperature

Soil CO$_2$ efflux was positively related to central soil temperature, but with a clear hysteresis effect (Fig. 5a–c), (i.e. at the same central soil temperature the observed soil efflux is higher during the warming phase than during the cooling phase). This occurs because the central temperature lags behind the temperature at a more superficial layer (cf. Fig. 3). Consequently, the single-source model typically leaves 10–30% of the efflux variance unexplained (Fig. 5d). In contrast, the dual-source model, which used $T_{\text{surf}}$ and $T_{\text{cent}}$ as predictors, consistently explained more than 95% of the variance in the organic samples leaving less than 5% unexplained (cf. also Table 2). Also in the mineral soils the dual-source model worked.

Fig. 3 Time series for soil CO$_2$ efflux (open circles, left axis), as well as surface and central temperature (diamonds and crosses, right axis) of one of the organic wet samples.

Fig. 4 Average soil water matric potential during the drying–rewetting experiment for each treatment. Error bars indicate one standard deviation. OC, OD, organic constantly wet, organic drying/rewetting; MC, MD, mineral constantly wet, mineral drying/rewetting.
Fig. 5  Scatter plots of soil CO₂ efflux vs. (a) central soil temperature and (b) soil surface temperature for the measurement cycles of Fig. 3. Labels indicate the integer hour of the respective day. (c) Soil CO₂ efflux as a function of surface and central temperature. The mesh shows the prediction from the dual-source model (fitted to these 3 days of data), data points (label as in a, b) are observed data ($R_{\text{soil, ref}} = 1.22 \pm 0.05 \, \mu mol \, m^{-2} \, s^{-1}$; $R_{\text{cent, ref}} = 1.03 \pm 0.04 \, \mu mol \, m^{-2} \, s^{-1}$; $Q_{10} = 2.72 \pm 0.06$; $r^2 = 0.96$, RMSE = 0.25). Arrows in a–c underline the trajectory with time showing the hysteresis effect. (d) Time series of coefficients of determination obtained with the dual- and the single-source model fitted to each diurnal cycle for one replicate of the organic wet treatment (OC). RMSE, root mean square error.

Table 2  Average coefficient of determination and NRMSE when modelling the diurnal courses of soil chamber CO₂ efflux using the single- or dual-source model for each treatment at the beginning and at the end of the experiment as well after the rewetting

<table>
<thead>
<tr>
<th></th>
<th>OC</th>
<th>OD</th>
<th>MC</th>
<th>MD</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Single</td>
<td>Dual</td>
<td>Single</td>
<td>Dual</td>
<td>Single</td>
</tr>
<tr>
<td>Coefficient of determination ($r^2$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Begin</td>
<td>0.65</td>
<td>0.97</td>
<td>0.80</td>
<td>0.96</td>
<td>0.51</td>
</tr>
<tr>
<td>End</td>
<td>0.83</td>
<td>0.98</td>
<td>0.84</td>
<td>0.98</td>
<td>0.73</td>
</tr>
<tr>
<td>Rewet</td>
<td>na</td>
<td>na</td>
<td>0.76</td>
<td>0.88</td>
<td>na</td>
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<tr>
<td>NRMSE</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Begin</td>
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<td>0.048</td>
<td>0.070</td>
<td>0.030</td>
<td>0.124</td>
</tr>
<tr>
<td>End</td>
<td>0.051</td>
<td>0.017</td>
<td>0.062</td>
<td>0.031</td>
<td>0.079</td>
</tr>
<tr>
<td>Rewet</td>
<td>na</td>
<td>na</td>
<td>0.088</td>
<td>0.079</td>
<td>na</td>
</tr>
</tbody>
</table>

OC, OD: organic constantly wet, organic drying/rewetting; MC, MD: mineral constantly wet, mineral drying/rewetting; NRMSE, normalized root mean squared error. The column ‘mean’ contains the mean quantity over all treatments.

considerably better explaining around 20% more of the variance than the single-source model (Table 2). In both soil types, the dual-source model also roughly halved the model error compared with the single-source model to below 10% in the mineral soils and to below 5% in the organic soils (except after rewetting).

Standardized respiration rates ($R_{\text{ref}}$)

The time courses of the soil CO$_2$ efflux standardized to 15°C ($R_{\text{ref}}$), that were yielded from the regression analysis performed for each diurnal cycle are depicted in Fig. 6. Soil CO$_2$ efflux decreased throughout the experiment for all treatments. The decrease in the wet treatments indicates the effect of incubation time during which substrate for decomposition diminishes. Initial rates of CO$_2$ efflux were around 3.5–4.5 µmol m$^{-2}$ s$^{-1}$ for organic soil, and 1–2 µmol m$^{-2}$ s$^{-1}$ for mineral soil. Soil CO$_2$ efflux rates for all treatments decreased rapidly during the first week, but subsequently declined at a slower rate. This behaviour is indicative of labile pool depletion, and was particularly pronounced in the mineral soil. Consequently, the proportion mineral $R_{\text{ref}}$ to organic $R_{\text{ref}}$ declined rapidly and stabilized at approximately 20% after 2 weeks of incubation.

A difference in efflux rates between wet and dry treatments developed during the first 25 days of the experiment, but did not increase (in absolute terms) after this period, although soil moisture continued to decline. The rapid rewetting of the dry samples at the end of the experiment led to an immediate increase in soil CO$_2$ efflux, which was initially higher than that of the corresponding wet samples, but lower than the

![Fig. 6](image-url)  
Fig. 6 Time series of $R_{\text{ref}}$ as fitted to each diurnal cycle in the laboratory incubation, for the organic layer (a) and mineral layer (b) soil cores. Filled symbols denote the constantly wet treatment; open symbols the drying–rewetting treatment. For clarity, estimation errors are summarized as ±1 average standard error of estimate for each treatment (OC, OD: organic constantly wet, organic drying/rewetting; MC, MD: mineral constantly wet, mineral drying/rewetting). $R_{\text{ref}}$ is derived from the dual-source model as $R_{\text{ref}} = R_{\text{surf,ref}} + R_{\text{cent,ref}}$ (cf. Eqn (2)). All, the incubation time effect, the drying–rewetting effect and the effect of the soil horizon are significant.

![Fig. 7](image-url)  
Fig. 7 (a) Partitioning of fluxes at reference temperature ($R_{\text{ref}}$ 15°C) between three different compartments in the constantly wet treatment (left) and the drying–rewetting treatment (right) at the beginning (Beg), end (End) of the drying period and after the rewetting (Rewet; see shaded areas in Fig. 6). (b) $R_{\text{ref}}$ estimate from parallel field measurements. The difference in respiration between the two treatments at the beginning of the incubation is because of the fact that the soil respiration was already reduced in the dry treatment over the averaging period. Error bars denote standard errors.

The dual-source model allowed us to tentatively separate the organic layer into a ‘surface’ layer and a ‘bulk organic’ layer, that could be added to fluxes measured on the mineral soil monoliths, resulting in three compartments (Fig. 7). At the beginning of the experiment, the R_{ref} summed up for the three compartments in the wet treatment compared favourably to the respective R_{ref} estimate from the field measurements, both at around 4 μmol m⁻² s⁻¹, with overlapping confidence intervals. However, after the 60–80 days of incubation, the total soil CO₂ efflux was nearly halved, and the relative contribution of the surface compartment declined slightly (from 36% to 29%), while the bulk organic compartments relative contribution increased (from 45% to 55%).

Total CO₂ efflux in the dry treatment was already reduced within the first 10 days of incubation, and by the end of the dry period total CO₂ efflux was reduced to about one-third of initial (wet) values. The surface compartment experienced a more than proportional decrease over this period, and eventually only constituted of 0.25 μmol m⁻² s⁻¹, or 20% of the total efflux. The difference between the two columns labelled ‘End’ in Fig. 7 document the effect of soil drying alone. Soil drying reduced the surface flux in absolute, but also relative terms. The reduction in flux from the bulk organic compartment is less severe, resulting in a larger relative contribution of 70% in the dry treatment, compared with 55% in the wet treatment. Rewetting approximately doubled the total flux, reaching slightly higher rates than the wet treatment suggesting a small rewetting effect. Here the surface compartment responded most strongly, raising its relative contribution from 20% to 36%.

Temperature sensitivity (Q_{10})

While the overall level of the soil CO₂ efflux (expressed as R_{ref}) exhibited clear treatment effects (incubation time effect, drying effect, mineral vs. organic soil effect), the temperature sensitivity (expressed as Q_{10}) was nearly invariant, regardless of the treatment (Fig. 8). Because of overall higher fluxes, the Q_{10} of organic samples could be determined with less uncertainty, fluctuating randomly between 2.5 and 3.0, while mineral sample Q_{10} values fluctuated around a similar mean but with higher variance. For both organic and mineral soils, no pure incubation time effect on the Q_{10} of soil CO₂ efflux could be detected. For both soils, a minimal but significant (organic soils: P = 0.049, mineral soils: P = 0.006, t-test) effect of the dry treatment is visible, resulting in slightly lower Q_{10}s in the dry treatment (Fig. 9). At the end of the dry period, the Q_{10} seems to drop more substantially, and significantly (P < 0.05) recovers after the rewetting. However, those changes remain within 0.4 Q_{10} units. The situation is summarized and compared with field estimates in Fig. 9. The dual-source model consistently estimates slightly higher Q_{10} values than the single-source model (non-hatched vs. hatched bars). The Q_{10} value for the field was derived from the same regression model and parameters as described for R_{ref} and calculated as the increase in CO₂ efflux for a temperature change from 10 °C to 20 °C to allow the comparison with the lab data. The Q_{10} estimates from the lab compare well with the field estimate of Q_{10} that was derived with a single-source model.

Discussion

A number of field and laboratory studies analysing the temperature dependence of soil respiration suffered...
from the problem that the respiration response to temperature is easily confounded by other factors (Davidson et al., 1998, 2000; Russell & Voroney, 1998; Koizumi et al., 1999; Morén & Lindroth, 2000; Savage & Davidson, 2001; Reichstein et al., 2002). This is most evident under uncontrolled field conditions, where soil water availability, radiation, vegetation production, and other factors co-vary with temperature. This problem has most recently been shown by Baath & Wallander (2003) who demonstrated that the results by Boone et al. (1998) – a higher temperature sensitivity of root compared the soil microbial respiration – were partly caused by interaction with vegetation activity.

In order to avoid confounding effects, laboratory experiments need to be carefully designed, as relative substrate availability changes during the experiment in different temperature treatments as discussed in detail by Reichstein et al. (2000). This problem can be circumvented by using a decomposition model where the rate constants are temperature dependent (e.g. Kätterer et al., 1998). However, decomposition models already contain a number of assumptions, which one might want to test independently. For instance, the temperature sensitivity of decomposition is usually assumed to be independent of SOM quality. This latter assumption of invariant temperature sensitivity has been criticized from very different perspectives. While Liski et al. (1999) empirically estimated that deep SOM (old low stable carbon) decomposition is independent of soil temperature, Bosatta & Agren (1999) argued that the temperature sensitivity should theoretically increase with decreasing carbon quality because the activation energy increases. It has also been found that the $Q_{10}$ of soil and ecosystem respiration empirically decreases with soil water deficit (Carlyle & Ba Than, 1988; Kutsch & Kappen, 1997; Reichstein et al., 2002). Our laboratory experiment allowed these problems to be studied on minimally disturbed soil cores under controlled conditions without confounding effects by varying the temperature at a much higher frequency than other factors change, while continuously observing the soil CO$_2$ efflux.

The observed decrease in soil respiration rate with increasing incubation time is in accordance with earlier studies, indicating a depletion of available substrate (Witkamp, 1966; O’connell, 1990; Cotrufo et al., 1995; Bottner et al., 1998; Bottner et al., 2000). Initial respiration rates were very similar to those in the field, which supports the fact that the internal structure of the samples remained largely unaltered (minimally disturbed samples). However, soil CO$_2$ efflux in the field includes root derived CO$_2$, as well as truly heterotrophic respiration (i.e. CO$_2$ derived from the decomposition of litter and SOM). The soil cores in the lab did contain roots, but as there was no new supply of photosynthates from aboveground by trees or grasses, this proportion soon diminished. The drop in respiration rates within the first week of incubation observed for all treatments is likely to be partly caused by the rapid decline of CO$_2$ flux from roots and labile root derived organic material. Field experiments where the supply of photosynthates to the roots has been suppressed by forest girdling (Högberg et al., 2001; Subke et al., 2004b) have shown that under these conditions, roots continue to respire starch reserves for several weeks. Our samples only included roots of diameters smaller than 2 cm, resulting in a smaller starch store compared with field conditions, and it is also likely that root growth and phloem transport had

**Fig. 9** (a) Average estimates of $Q_{10}$ in the organic layer (left) and the mineral layer (right), at the beginning (beg), end (end) of the drying period and after the rewetting (Rewet). Filled bars are from constantly wet treatment, open bars from drying-rewetting treatment. Hatched or striped bars represent results from the dual-source model, solid bars from the single-source model. (b) $Q_{10}$ estimate from parallel field measurements using the single-source model. Error bars denote standard errors. Only the effect of the dry treatment is significant.
still not reached high values in this montane forest at the time of sampling.

The effect of the soil drying is expected and confirms the results of earlier studies (Orchard & Cook, 1983; Howard & Howard, 1993; Lomander et al., 1998). The drying was not extreme (e.g. not up to the permanent wilting point), but nevertheless respiration was clearly reduced by approximately 50%. Such reduction is expected by common models that relate soil microbial activity to the logarithm of soil water potential (pF-value) with a maximum at field capacity (−250 hPa; pF 2.3) and zero respiration at the permanent wilting point (−15 000 hPa; pF 4.2) (e.g., Andrén et al., 1992; Rodrigo et al., 1997) where in our study the soil water potential dropped to between −1000 and 2000 hPa (pF 3–3.3). It is noteworthy that the difference in soil respiration between wet and dry treatments hardly increased after 30 days of incubation. Although speculative, this may indicate that after a certain time substrate limitation becomes more and more co-limiting to respiration, so that the sensitivity to water availability declines. Rewetting has been reported to cause soil CO2 efflux rates that exceed those rates before drying (Redeker et al., 2004; Xu & Baldocchi, 2004). This so-called Birch effect (Birch, 1958) is explained by remineralization of dead microbes and release of easily decomposable substrate through rewetting. In our experiment, this effect was confirmed, as CO2 efflux rates after rewetting exceeded those of the wet samples at the same time. In addition to the pool of labile C supplied from dead microbial biomass, a portion of the extra respiration may be caused by decomposition of SOM which had been ‘saved’ under drought conditions, when microbial activity was limited by water rather than substrate. That a labile carbon fraction had mobilized is supported by the fact, that respiration rate dropped within 10 days of the rewetting, even though samples were kept constantly wet thereafter.

According to our analysis with the dual-source model, the surface layer showed the largest variation with incubation time and the most pronounced responses to drying–rewetting. Thus, our study calls attention to the importance of fluxes from the soil surface. In particular, superficial rewetting events that trigger surface respiration may not be accounted for by models that are driven by observations at 5 or 10 cm depth or that treat the soil as monolayer ‘bucket’. Reichstein et al. (2003) and Xu & Baldocchi (2004) experienced these problems with rain events after drought, when fluxes were higher than expected according to soil moisture at 10 cm. Changes in relative contributions from different soil compartments may well change the apparent $Q_{10}$ of soil respiration, when CO2 efflux data are correlated with a temperature at a fixed position (discussed in Subke et al., 2003). Such a correlation may result in a wide range of observed apparent $Q_{10}$ values (e.g. Janssens & Pilegaard, 2003), which have to be treated with caution before conclusions about soil physiological responses to temperature are drawn. Also with respect to results from Irvine & Law (2002), we propose that ecosystem models operating at subdaily to daily time steps should comprise a surface, a main root zone and – at least in forests – a deep soil layer to account for different dynamics in different compartments.

Our results from the dual-source model are somewhat exploratory and we were not able to provide a final validation of the surface flux estimate. But we show that with such a still simple approach, the descriptive power is clearly enhanced, and the results we obtained concerning relative contributions are quite plausible: (1) The surface layer consisting of fresh grass and needle litter, very likely contains the highest proportion of labile SOM, and thus our result that surface flux declines more strongly than the flux from the bulk soil is reasonable. (2) Similarly, our observation (derived from the dual-source model) that the surface layer responds most sensitively to the drying–rewetting treatment is conceivable, because the surface layer dries up most severely. Two field studies conducted at the same site showed conflicting results concerning flux contributions from the organic and mineral layers. While Buchmann (2000) concluded from direct measurements following the removal of organic horizons that the majority of respired CO2 originates from the mineral layer, Subke et al. (2003) argued that the correlation between temperature and surface efflux suggest that the organic layer has the larger contribution to the total soil CO2 efflux. (The conflict between the results of both field studies is discussed in Subke et al., 2003). Thus, we suggest that such inverse estimation of flux partitioning between different compartments should be further investigated and could be validated nondestructively (e.g. with isotope-labeling studies).

One of the main questions posed in the current study was about the commonly assumed invariance of the temperature sensitivity of soil respiration processes, which has recently been criticized. The effect of organic matter age on the temperature sensitivity of soil respiration was inferred indirectly only, but from two perspectives: (a) With incubation time the relative contribution of young SOM pools declines and the contribution of older pools increases, thus if older pools had a different temperature sensitivity the $Q_{10}$ should change with incubation time. (b) The mineral-SOM is older than the organic layer carbon, thus the mineral soil should have had a different $Q_{10}$ than the organic layer, as (e.g. suggested by Liski et al. 1999). As virtually
no effects of incubation time or soil layer on the $Q_{10}$ of soil respiration were detected, our study suggests no or only minor effects of SOM age on the $Q_{10}$ of soil respiration. A limitation to this conclusion is that we did not explicitly determine the age of the carbon respired and we cannot infer the temperature sensitivity of very old pools, if their contribution to the overall flux is very small.

The effect of soil water availability on the temperature sensitivity of decomposition of SOM was statistically significant, but modest ($<0.4$ $Q_{10}$ units on average) at the levels of drying in this experiment and much less drastic than suggested by recent field studies (Xu & Qi, 2001; Reichstein et al., 2003). However, if the results are somewhat equivocal, as (a) there might be a threshold type of relationship between $Q_{10}$ and soil water availability and (b) the drying might not have been advanced enough to pass such a threshold. The drop of $Q_{10}$ at the end of the drying period is indicative of this, but is too singular, as we did not continue the drying past this point, and this possibility should be investigated further.

Conclusions

Our study analysed the temperature sensitivity of soil respiration in the laboratory under minimization of confounding effects that often occur under field conditions and separated the effects of soil moisture, soil horizon and decomposition dynamics (incubation time). Under our conditions we did not find evidence of important changes of the direct sensitivity of soil respiration to temperature in response to the mentioned factors. This contrasts recent results from field studies and shows that one must be careful with interpretation of statistical results from ecosystem level studies, as these results can be ‘emergent properties’ that do not hold at the lower organizational level (e.g. $Q_{10}$ of soil respiration vs. $Q_{10}$ of decomposition rate constants in a process model). From our experiment we cannot conclude that in process models the temperature sensitivity of rate constants should either differ between organic and mineral layer carbon, or should change along ongoing decomposition of SOM. Our results demonstrate that laboratory experiments, which are commonly criticized for being unnatural, should be realized as a successful complementary tool to field measurements, as they allow a more elaborate elucidation of confounded factors. The disturbance caused by sampling of soil cores can be minimized if the structure of the soil is retained, and is more than compensated by the possibility of controlling abiotic conditions in the laboratory.

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