



# Temperature dependence of carbon mineralisation: conclusions from a long-term incubation of subalpine soil samples

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## Abstract

Carbon mineralisation from soil samples was analysed during a 104-day laboratory incubation at 5, 15 and 25°C. The samples were taken from the upper horizon of each of two topographically different micro-sites (gully: A-horizon; ridge: Oe/Oa-layer) at the Stillberg Alp close to Davos in the Swiss Central Alps. On both the soils, carbon mineralisation rates decreased substantially with incubation time (e.g. from 0.3 to 0.18 mg CO<sub>2</sub>-C d<sup>-1</sup> g<sup>-1</sup> organic carbon in the Oe–Oa-layer and from 0.6 to 0.2 mg CO<sub>2</sub>-C d<sup>-1</sup> g<sup>-1</sup> organic carbon at 25°C in the A-horizon). Carbon mineralisation was well described by a first-order kinetic two-compartment model and a functional temperature dependence of the rate constants. Both temperature models, the exponential  $Q_{10}$ -function and a quadratic function described the cumulative C-mineralisation correctly within one standard error of estimate (SE) of the measured values. However, the  $Q_{10}$  model gave a slightly better fit to the data, and  $Q_{10}$ -values of 2.5 and 2.8 were computed for the rate constants of the organic layer and the A-horizon, respectively. While the temperature dependence of the (time independent) rate constants of mineralisation appeared to be well-defined, this was not the case for  $Q_{10}$  of the instantaneous respiration rates, which were a non-linear function of incubation time. The general pattern of fluctuation of the instantaneous  $Q_{10}$ -values was in accordance with the results computed by the models, and can be explained by the parallel decomposition of two different soil organic matter pools. To avoid the effects of the time of the respiration measurement on the calculated  $Q_{10}$ , it is recommended to analyse the whole time series in order to infer the temperature dependence of respiration, or at least to standardise the time at which soil respiration is measured. In a second part of the study, our laboratory results temperature effects were extrapolated to the field, using measurements of soil temperature as driving variables to a recently developed carbon balance model. Carbon mineralisation was roughly estimated to be 52–84 g C m<sup>-2</sup> year<sup>-1</sup> for the gullies and 70–125 g C m<sup>-2</sup> year<sup>-1</sup> for the ridges. Unexpectedly, the choice of the temperature model had a great influence on the estimate of annual carbon mineralisation, even though models differed only little concerning the fit to the laboratory incubation data. However, it could be shown that winter-time mineralisation probably accounted for at least 22 and 40% of the whole-year mineralisation on the ridges and the gullies, respectively, and therefore, should not be neglected in carbon-balance studies. © 2000 Elsevier Science Ltd. All rights reserved.

**Keywords:** CO<sub>2</sub> Efflux; Decomposition; Modelling; Soil carbon; Temperature dependence

## 1. Introduction

Soil organic carbon is a substantial component of global carbon pools (e.g. Raich and Schlesinger, 1992; Kirschbaum, 1993). Thus, understanding and predicting the response of soil carbon to changes in global temperature is critical, particularly since increased

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release of respired carbon dioxide (CO<sub>2</sub>) to the atmosphere has the potential to exacerbate global warming (Schimel et al., 1994).

While a significant correlation between soil temperature and carbon mineralisation is well established (see reviews by: Singh and Gupta, 1977; Raich and Schlesinger, 1992; Lloyd and Taylor, 1994; Kirschbaum, 1995; Kätterer et al., 1998), there is no agreement about which function to use to describe the relationship between soil carbon mineralisation and temperature. From laboratory experiments, two main approaches can be distinguished to obtain data for fitting functions: first, comparing instantaneous CO<sub>2</sub> efflux rates at different soil temperatures (e.g. Ross and Cairns, 1978; Winkler et al., 1996) and second, an analysis of the time series of CO<sub>2</sub> efflux using a decomposition model (e.g. Blet-Charaudeau et al., 1990; Updegraff et al., 1995; Lomander et al., 1998). Each approach has certain disadvantages: When measuring instantaneous CO<sub>2</sub> efflux one has to cope with the problem that the apparent temperature sensitivity of CO<sub>2</sub> efflux may be dependent on the point in time when the flux is measured, implying that studies are not comparable when measuring respiration at different pre-incubation times. On the other hand, when measuring longer term time series CO<sub>2</sub> efflux, artificial conditions may arise (e.g. the formation of toxic metabolic by-products, see Kirschbaum, 1995). These problems introduce uncertainty into the estimation of parameters for temperature response functions of decomposition used in ecosystem and soil organic matter models. In addition, the different submodels of soil organic matter decomposition use functions of quite dissimilar shape (Rodrigo et al., 1997).

In this case study, we analyse the temperature dependence of carbon mineralisation during a long-term laboratory incubation using (1) instantaneous CO<sub>2</sub> efflux rates and (2) a decomposition model. First, we show how much the  $Q_{10}$ -values of instantaneous rates change during the incubation and we discuss how to best analyse data from laboratory incubation experiments. Second, we examine the uncertainty of soil carbon efflux predictions in the field, which arises from the choice of the temperature response function. For this, we fitted two different temperature response functions to the laboratory incubation data, incorporated them into a simple carbon balance model (Andrén and Kätterer, 1997), applied this model to temperature data from the field where the soil samples have been taken, and compared the outputs of the different temperature functions.

## 2. Materials and methods

The study area is located in the forest-tundra eco-

tone on a north-east exposed steep slope (41° inclination) of the Dischma valley near Davos (Switzerland) (09° 52' E, 46° 47' N; 2000–2200 m a.s.l.). The climate is characterised by an annual precipitation of 1047 mm. The mean annual temperature is 1.4°C (Schönenberger and Frey, 1988). Parent soil material of the research area is gneiss, and the slope is structured by ridges and gullies, which exhibit completely different soil types and humus forms (Blaser, 1980). The ridges are covered by *Vaccinium*-dwarf-shrub heath while the gully vegetation is dominated by *Calamagrostis villosa* L.

Three ridges and three gullies were selected to study the upper soil horizons, i.e. the Oe/Oa-layer and the A-horizon, respectively. The plots (3 m × 9 m) on the sites were chosen in June 1996. At each plot, two soil samples were taken, each consisting of 10 subsamples. All chemical analyses refer to sieved (2 mm) and oven-dry soil. Organic carbon and total nitrogen content were determined by an elemental analyser (Carlo Erba NA 1500), and pH in 0.01 M CaCl<sub>2</sub> (vol<sub>Soil</sub>:vol<sub>Solution</sub> = 1:5) using a glass electrode (Sparks, 1996).

### 2.1. Soil respiration measurements

Soil respiration was measured on fresh soil samples, which had been stored in polyethylene bags at 4°C for maximally 10 days. After sieving to 2 mm and adjusting soil moisture to 60% WHC (Schinner et al., 1993), the soil samples were incubated in 2.4 l vessels at 5, 15 and 25°C. However, for the 5 and 15°C treatment of the A-horizon samples, we used 0.5 l vessels to achieve measurable CO<sub>2</sub>-concentrations within a certain time span. The quantity of the soil samples incubated was equivalent to 25 g dry soil. The depth of the soil in the vessel approximated 1.5 cm. A closed gas-cycle apparatus including an IRGA was used to measure CO<sub>2</sub>-flux from the soil samples according to Klimanek (1994). After 16 days, sampling frequency was reduced from two to one time per eight days during the experimentation period of 104 days. CO<sub>2</sub>-concentrations were converted into units of mass CO<sub>2</sub> per dry mass soil by applying the common gas law according to Klimanek (1994). After each measurement, the vessels were flushed with air and then CO<sub>2</sub> was depleted (soda lime trap in the gas-cycle). This assured that the CO<sub>2</sub>-concentration in the vessels never exceeded 1%. The water loss was determined gravimetrically and did not exceed 2%. Thus, no water had to be added to maintain a nearly constant water content. All laboratory measurements were performed in duplicate.

### 2.2. Data analysis

For each site type (gully and ridge) and temperature, the mineralisation curves of the six field replicates were

averaged for further analyses. We used three different methods to analyse the dependence of carbon mineralisation on temperature.

1. A time series of the  $Q_{10}$ s of the instantaneous soil  $\text{CO}_2$ -efflux rates ( $R$ ) was determined by the simple equations  $Q_{10}(t) = R(t, 25^\circ\text{C})/R(t, 15^\circ\text{C})$  and  $Q_{10}(t) = R(t, 15^\circ\text{C})/R(t, 5^\circ\text{C})$ , respectively.
2. A first-order kinetic two-compartment model

$$C_{\min}(t) = C_1 \cdot (1 - e^{-k_1 t}) + C_2 \cdot (1 - e^{-k_2 t}) \quad (1)$$

(Andr  n and Paustian, 1987) was fitted to the mean cumulative carbon mineralisation data for each site and temperature, where  $C_{\min}(t)$  is the amount of carbon mineralised until time  $t$  [ $\text{mg CO}_2\text{-C g}^{-1}$  organic C],  $C_1$  is the mass of the labile carbon fraction [ $\text{mg C g}^{-1}$  organic C],  $C_2$  is the mass of the recalcitrant carbon fraction [ $\text{mg C g}^{-1}$  organic C]. It is assumed that  $C_1 + C_2 = 1000 \text{ mg C g}^{-1}$  organic C, i.e. that labile and recalcitrant fraction sum up to total organic carbon in the soil sample.  $k_1$  and  $k_2$  are the first-order decomposition rate constants for the labile and recalcitrant fraction [ $\text{d}^{-1}$ ], respectively. The parameters were estimated using non-linear regression analysis (NLIN, SAS Institute Inc., 1982). Standard errors of the estimated parameters were not computed because of their inaccuracy due to autocorrelation of cumulative measurements in time series (c.f. Hess and Schmidt, 1995). Hereafter, this approach is referred to as the ‘*separate model*’, because the model was separately applied to each temperature treatment. From the fitted model, a time series of respiration rates were calculated as the derivatives of Eq. (1), and the time series of  $Q_{10}$ -values of modelled respiration were computed, as in (1).

3. ‘*Combined model*’: Cumulative carbon mineralisation was simultaneously modelled both as a function of time and soil temperature, i.e. a ‘*combined model*’:

$$C_{\min}(t, T) = C_1 \cdot (1 - e^{-r(T)k_1(T_{\text{ref}})t}) + C_2 \cdot (1 - e^{-r(T)k_2(T_{\text{ref}})t}) \quad (2)$$

where  $r(T)$  is a scaling function relating mineralisation rate at temperature  $T$  to the rate at  $T_{\text{ref}}$  and the other parameters as in Eq. (1). In this approach we assumed that both rate constants are equally dependent on temperature. For the respiration rates computed with this ‘*combined model*’, a time series of  $Q_{10}$ -values of modelled respiration rates were calculated, as in 1 and 2.

Two different  $r(T)$ -functions were examined: the common  $Q_{10}$ -model

$$r(T) = Q_{10}^{\frac{T-T_{\text{ref}}}{10}} \quad (3)$$

and a quadratic function (Ratkowsky et al., 1982)

$$r(T) = \begin{cases} \frac{(T-T_{\min})^2}{(T_{\text{ref}}-T_{\min})^2} & \text{for } T \geq T_{\min} \\ 0 & \text{for } T < T_{\min} \end{cases} \quad (4)$$

which is based on a temperature ( $T_{\min}$ ) below which biological activity ceases. Therefore, this model will be called  $T_{\min}$ -model. The  $T_{\min}$ -model implies an increasing  $Q_{10}$  with decreasing temperature. As shown above, parameters were estimated using non-linear regression (NLIN, SAS Institute Inc., 1982) and the fits of the different models to these data were evaluated by calculating the coefficient of determination ( $R^2$ ) and the adjusted  $R^2$  ( $R^2_{\text{adj}}$ ), (Kv  lseth, 1985).

### 2.3. Extrapolation to the field

The Introductory Carbon Balance Model (ICBM, Andr  n and K  tterer, 1997) was used for extrapolations of the laboratory results to the field:

$$\frac{d}{dt}C_Y(t) = i - r \cdot k_1 \cdot C_Y(t) \quad (5)$$

and

$$\frac{d}{dt}C_O(t) = r \cdot h \cdot k_1 \cdot C_Y(t) - r \cdot k_2 \cdot C_O(t) \quad (6)$$

This model assumes two organic C fractions ( $C_Y$ : young, i.e. labile,  $C_O$ : old, i.e. stabile), which are decomposed by first-order kinetics and where the fraction  $h$  of the outflux from  $C_Y$  ( $r \cdot k_1 \cdot C_Y$ ) is transformed into  $C_O$  (i.e.  $h$  = humification) while the old fraction is entirely decomposed to  $\text{CO}_2$  ( $r \cdot k_2 \cdot C_O$ ). Litter input  $i$  enters the system through the labile carbon pool ( $C_Y$ ).

Computation of monthly decomposition rate constants: The rate constants of organic carbon decay can be altered by a factor  $r$  due to abiotic conditions. In our study, only the response to temperature was included, and  $r$  was normalised for  $15^\circ\text{C}$ , the mean temperature of the laboratory incubations. Monthly  $r$ -factors for the field were estimated from monthly means of daily maximum and minimum soil temperatures at 5 cm depth ( $T_{\text{daymax}}$ ,  $T_{\text{daymin}}$ ) at the site (Turner et al., 1975), which were first disaggregated to hourly values in order to avoid aggregation errors (c.f. Lischke et al., 1997). The diurnal course of soil temperatures was approximated by an hourly evaluation of the sine function

$$T(t) = \frac{T_{\text{daymax}} + T_{\text{daymin}}}{2} + \frac{T_{\text{daymax}} - T_{\text{daymin}}}{2} \cdot \sin\left(2\pi \cdot \frac{t}{24}\right) \quad (7)$$

For each hour of the day, hourly  $r$ -factors were calculated according to both, the  $Q_{10}$  and the  $T_{\text{min}}$  functions (Eqs. (3) and (4)). The setting of the other ICBM parameters was done as follows: The rate constant  $k_2$  was directly taken from the laboratory incubation, while the rate constant  $k_1$  was chosen so that the ratio  $k_1/k_2$  was the same as in original calibration of Andrén and Kätterer (1997). The humification coefficient was set to 0.13 for the gullies (non-woody debris, as in original calibration), and to 0.3 for the ridge (woody shrubs). The total soil carbon storage in the field has been measured previously (Bednorz et al., 2000), so that the other parameters could be estimated assuming steady state for total organic soil C ( $C_T$ )

$$C_{T, \text{ss}} = \frac{i \cdot (1/k_1 + h/k_2)}{r} \Leftrightarrow i = C_{T, \text{ss}} \cdot \frac{r}{(1/k_1 + h/k_2)} \quad (8)$$

$$C_{Y, \text{ss}} = \frac{i}{r \cdot k_1} \quad (9)$$

and

$$C_{O, \text{ss}} = \frac{h \cdot i}{r \cdot k_2} \quad (10)$$

where  $C_{T, \text{ss}}$ ,  $C_{O, \text{ss}}$ ,  $C_{Y, \text{ss}}$  and  $i$  are the steady-state stocks of total, old and young carbon, and the annual carbon input, respectively, in the field. The complete parameterisation of the ICBM is shown in Table 1. The monthly input  $i_M$  to the system was approximated by a sinus function with a mean of  $i/12$ , with the maximum of litter input (180% of average litter input)

occurring in October and the minimum (20% of average litter input) occurring in April. With these parameters, the ICBM was run applying a monthly time step ( $t = 1/12$  year), and the monthly carbon mineralisation follows from the mass balance according to Eqs. (5) and (6)).

### 3. Results

The physical and chemical characteristics of the investigated soil horizons are given in Table 2. After 104 days of incubation at 15°C, about 1.5% of the carbon in the A-horizon of the gullies and nearly 1% of the carbon in the organic layer of the ridge had been mineralised (Fig. 1 a). The respiration rates clearly declined with incubation time at all temperatures, at least during the first 50 days (Fig. 1b). Both, the absolute respiration rates and the shape of the time courses differed between the temperature treatments: While at 5°C, respiration rates declined relatively slowly and constantly with time, the decline at 15°C and particularly at 25°C was much faster and occurred mainly during the first half of the incubation (Fig. 1b).

Consequently, concerning the instantaneous  $Q_{10}$  of soil respiration, the effects of incubation time and the temperature interval interacted (Fig. 2). On average, the  $Q_{10}$  in the interval 5–15°C was higher than the 15–25°C interval at the beginning of the incubation, but lower at the end. This behaviour was also reproduced by the models, but due to fluctuations in the measured data the explained variance was below 50%, with one exception (Fig. 2, Table 3). The goodness of model fit to the measured  $Q_{10}$ -time series decreases in the order ‘separate model’ > ‘combined model’ ( $Q_{10}$ ) > ‘combined model’ ( $T_{\text{min}}$ ).

The two-compartment model properly described the measurements, ( $R_{\text{adj}}^2 > 0.98$  for the cumulative curves and  $> 0.8$  for respiration rates). Model estimates were nearly always within 1 SE of the cumulative data

Table 1

Parameterisation of the Introductory Carbon Balance Model (ICBM) in this study for the extrapolation of laboratory results to the field. For meaning of parameters, see text

Parameter	Value		Source
	Ridge	Gully	
$k_1$ (at 15°C)	3.72 (year <sup>-1</sup> )	3.84 (year <sup>-1</sup> )	Set relative to $k_2$ , $k_1/k_2$ as in Andrén and Kätterer (1997)
$k_2$ (at 15°C)	0.0230 (year <sup>-1</sup> )	0.0292 (year <sup>-1</sup> )	From laboratory incubation
$h$	0.30	0.13	c.f. Andrén and Kätterer (1997)
$C_{T, \text{ss}}$	5.83 (kg m <sup>-2</sup> )	1.25 (kg m <sup>-2</sup> )	Measured from field samples
$C_{Y, \text{ss}}$	0.14 (kg m <sup>-2</sup> )	0.07 (kg m <sup>-2</sup> )	Computed (Eq. (9))
$C_{O, \text{ss}}$	5.69 (kg m <sup>-2</sup> )	1.18 (kg m <sup>-2</sup> )	Computed (Eq. (10))
$r$	Varying according to temperature model		Computed (Eqs. (3) and (4))
$i$	0.125 (kg m <sup>-2</sup> yr <sup>-1</sup> )	0.083 (kg m <sup>-2</sup> yr <sup>-1</sup> )	Computed (Eq. (8))

Table 2

Physicochemical parameters of the soil samples. Numbers in parenthesis are standard deviations. For more information on the spatial variability of soil parameters on the sites, see Bednorz et al. (2000)

Parameter	Ridge (organic layer)	Gully (A-horizon)
pH (CaCl <sub>2</sub> )	3.0 (0.05)	3.6 (0.07)
Organic C (g kg <sup>-1</sup> )	403.1 (49.4)	56.5 (16.4)
N <sub>t</sub> (g kg <sup>-1</sup> )	13.3 (2.2)	3.7 (0.8)
C/N-ratio (g g <sup>-1</sup> )	30.3 (2.9)	15.2 (2.0)
Bulk density (g fine soil cm <sup>-3</sup> total volume)	0.13(0.07)	0.22 (0.03)
Organic C (kg m <sup>-2</sup> )	5.83 (3.84)	1.25 (0.12 <sup>a</sup> )

<sup>a</sup> Without variability due to rock outcrop.

(Fig. 2a). The same held for the separate model predictions of respiration rates during the second half of the incubation (Fig. 2b). The combined model (with the explicit  $Q_{10}$ -dependence of the rate constants) described the data nearly as well as the separate model, where no assumption on the temperature dependence was made. In contrast, using the  $T_{\min}$ -model, model predictions deviated notably from the measurements, particularly in the beginning and the end of the incubation.

The optimised parameters for the ‘combined’ models are shown in Table 4. For the separate model, the asymptotic correlation between the parameter values was around 0.9, i.e. the parameters cannot be independently interpreted, and therefore, are not shown. The  $T_{\min}$ -model yielded a temperature  $T_{\min}$  of  $-5.1$  and  $-6.2^{\circ}\text{C}$ , at which decomposition ceases, the  $Q_{10}$ -model yielded a  $Q_{10}$ -values of 2.5 and 2.8. The parameter estimates of  $C_1$ ,  $k_1$  and  $k_2$  at the reference temperature  $T_{\text{ref}}$  differed considerably between the two models, but relative differences between the sites were similar among the models (Table 4).

### 3.1. Extrapolation to the field

The annual course of the monthly average of the daily maximum and minimum temperatures differs distinctly between the gullies and ridges (Fig. 3). In winter, the ridge temperature drops below zero, whereas the gully soil temperatures mostly stay above zero. The calculated monthly  $r$ -factors for the mineralisation in winter differ considerably among the models (up to

a factor of 26 lower for  $T_{\min}$ -model compared to  $Q_{10}$ -model), while in summer the difference is only around 10%. The average annual  $r$ -factor is about 0.5–0.6 times lower in the  $T_{\min}$ -model than in the  $Q_{10}$ -model. Of course, like the monthly  $r$ -factors carbon mineralisation is affected by the model choice (Fig. 4). For example, for the ridge, a more than three-fold higher C-mineralisation during the first half of the year is predicted by the  $Q_{10}$ -model compared to the  $T_{\min}$ -model (42 and 12 g C m<sup>-2</sup>, respectively).

The predicted annual carbon mineralisation ranges between 52 and 84 g C m<sup>-2</sup> for the gully, and between 70 and 125 g C m<sup>-2</sup> for the ridge (Fig. 4), depending on the temperature function. The model further predicted that in the ridges outside the growing season (November to the end of May, c.f. Schöenberger and Frey, 1988) at least 22 and 45% of the annual carbon mineralisation occurs according to the  $T_{\min}$  and  $Q_{10}$  function, respectively. For the gullies, even 53% of the annual carbon mineralisation are predicted by the  $Q_{10}$  function to occur outside the growing season.

## 4. Discussion

### 4.1. Laboratory incubation

The carbon mineralisation rates were clearly dependent on soil temperature between 5 and 25°C. The temperature dependence was best described by the  $Q_{10}$ -model as compared to the  $T_{\min}$ -model, implying a constant  $Q_{10}$  with temperature between 5 and 25°C.

Table 3

Goodness-of-fit between measured and modelled time series of  $Q_{10}$  of soil respiration from ridge and gully samples (‘separate’ means model where each temperature was treated separately when fitting, i.e. no temperature model was assumed c.f. Section 2.2).

Measure	Ridge			Gully		
	Separate	$Q_{10}$ - model	$T_{\min}$ - model	Separate	$Q_{10}$ - model	$T_{\min}$ - model
$R^2$	0.45	0.34	0.01	0.64	0.44	0.12
MD <sup>a</sup>	0.16	0.17	0.30	0.27	0.31	0.34

<sup>a</sup> Mean absolute deviation.

This contradicts the general trend of an increasing  $Q_{10}$  with decreasing temperatures (Lloyd and Taylor, 1994; Kirschbaum, 1995). However, it has to be noted that this general trend is an average over many soil and ecosystem types and even in these reviews there are

several subsets with constant  $Q_{10}$ -values. In the literature, there is even evidence of increasing  $Q_{10}$ -values with temperature (Nadelhoffer et al., 1991; Howard and Howard, 1993). The absolute values of the  $Q_{10}$  in our study (2.5–2.8) are slightly above the median of

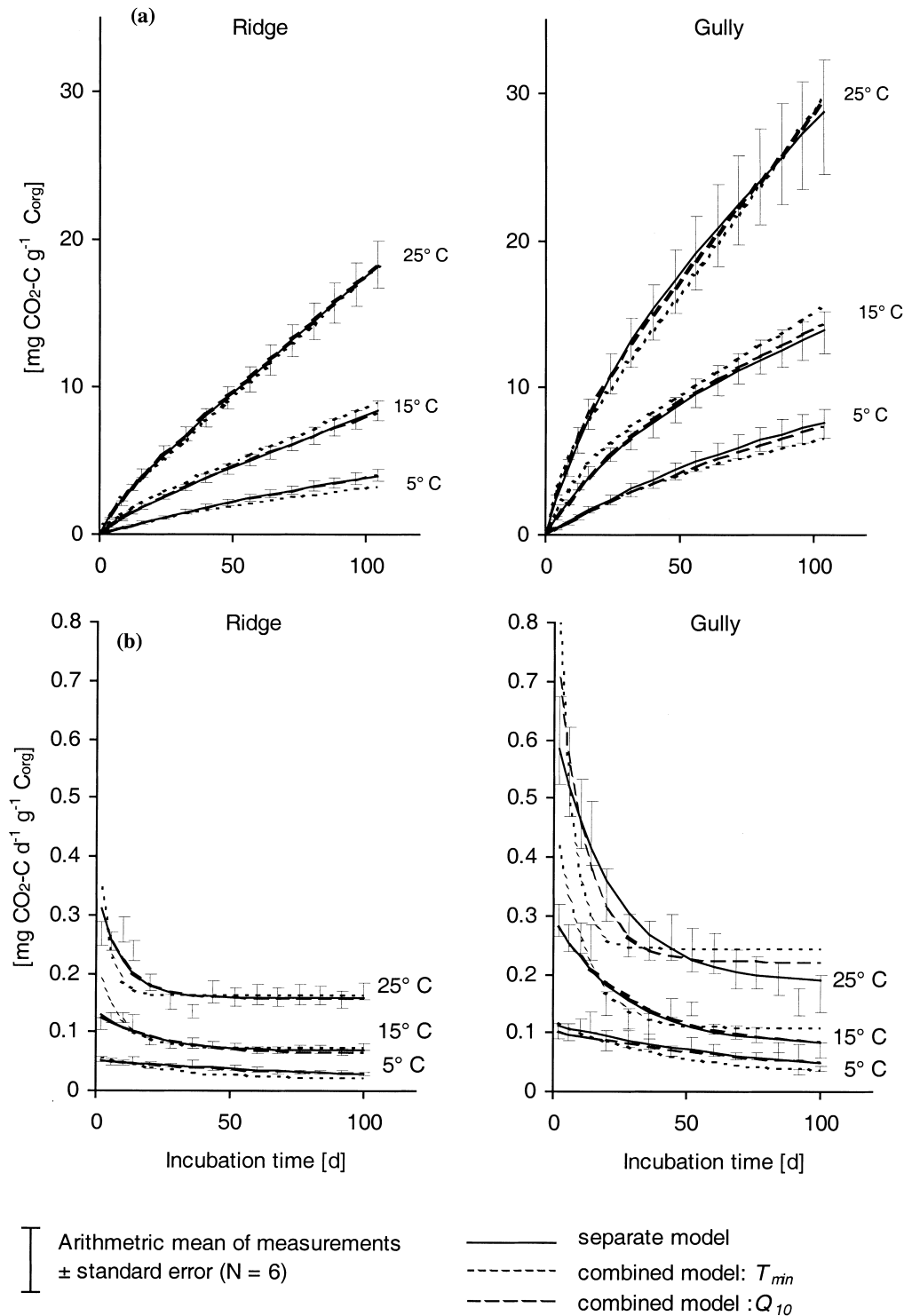


Fig. 1. Measured and modelled cumulative carbon mineralisation (a), and respiration rates (b) of gully-Ah- and ridge-organic-layer samples at 5, 15 and 25°C. For model definition, see Section 2.2.

2.0–2.4 given by literature reviews (Raich and Schlesinger, 1992; Kätterer et al., 1998). In view of the highly variable results of the studies, there seems to be little chance for a general description of the temperature dependence and absolute  $Q_{10}$ -values. Interactions with other factors, which influence the mineralisation response to temperature, have to be considered, such as, substrate quality (e.g. Bunnell et al., 1977a, 1977b;

Anderson, 1991) and soil moisture (e.g. Svensson, 1980; Anderson, 1991; Howard and Howard, 1993).

In addition, our study revealed an additional factor that may explain differences in  $Q_{10}$ -values reported for C-mineralisation studies, i.e. the dependence of the instantaneous C-mineralisation rate on the incubation time. The two-compartment model gives a plausible explanation for the dynamics of

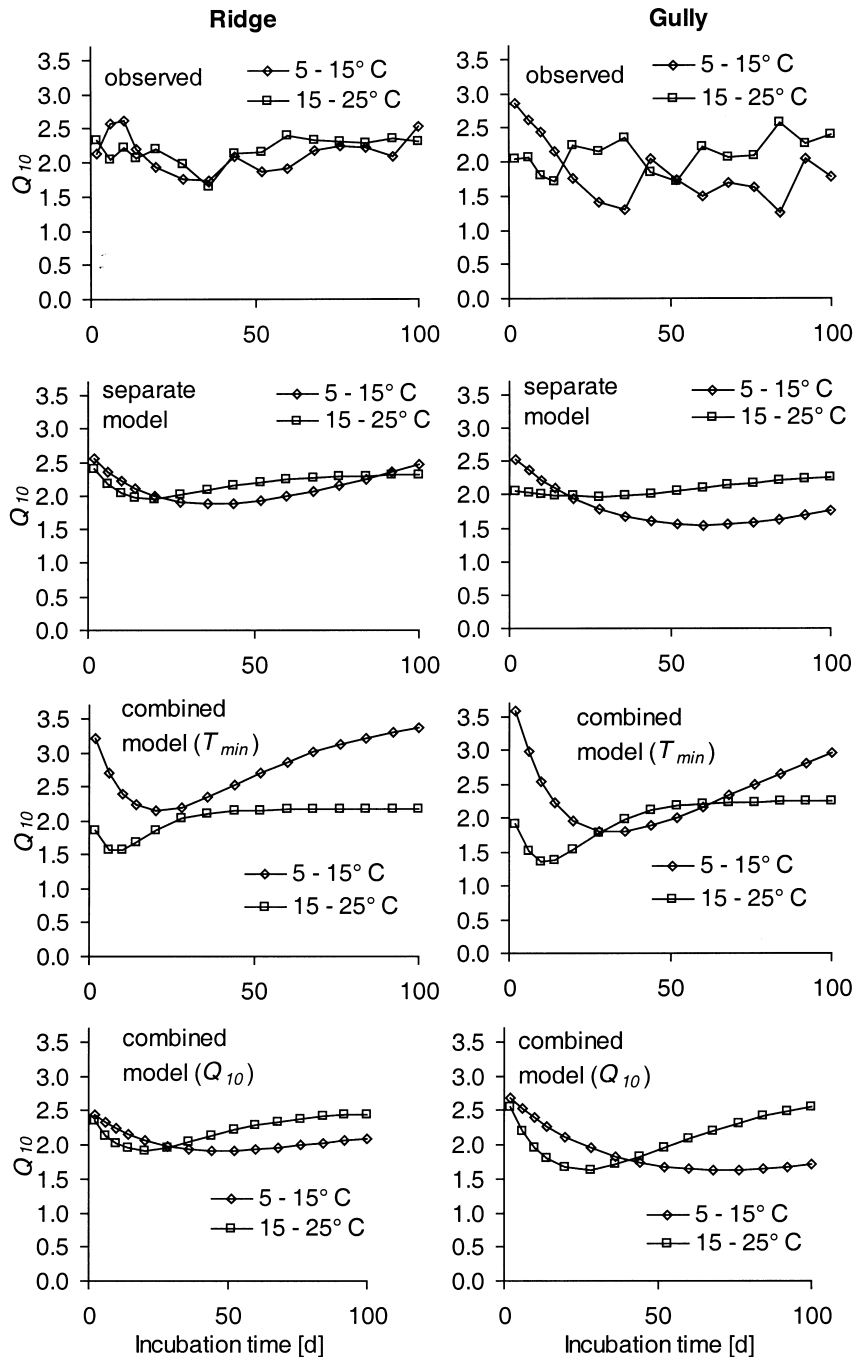


Fig. 2. Time series of the instantaneous  $Q_{10}$  of soil respiration within two temperature intervals during incubation of ridge and gully samples, observed and predicted by the different models. For model definition, see Section 2.2.

Table 4  
Optimised parameters of the ‘combined’ mineralisation models  
( $T_{\text{ref}} = 15^{\circ}\text{C}$ )

Parameter	Ridge		Gully	
	$Q_{10}$ -model	$T_{\text{min}}$ -model	$Q_{10}$ -model	$T_{\text{min}}$ -model
$C_1$ ( $\text{mg g}^{-1}$ )	1.70	1.18	6.15	4.07
$k_1$ at $T_{\text{ref}}$ ( $\text{d}^{-1}$ )	0.041	0.120	0.034	0.091
$k_2$ at $T_{\text{ref}}$ ( $\text{d}^{-1}$ )	$6.3 \times 10^{-5}$	$7.5 \times 10^{-5}$	$8.0 \times 10^{-5}$	$10.9 \times 10^{-5}$
$Q_{10}$	2.50	n.a. <sup>a</sup>	2.77	n.a.
$T_{\text{min}}$ ( $^{\circ}\text{C}$ )	n.a.	−6.2	n.a.	−5.1

<sup>a</sup> n.a. = not applicable.

the  $Q_{10}$  for instantaneous C- mineralisation rates. At higher temperatures, the easily decomposable fraction will be mineralised more quickly than at lower temperatures. That implies that after a certain time there will be more easily decomposable matter left over in the low-temperature treatment than in the high-temperature one. The result is a relatively higher soil respiration rate in the low-temperature treatment after a certain time, i.e. a decreasing  $Q_{10}$  with incubation time. When the easily decomposable fraction also in the low-temperature treatment is nearly completely decayed, then the  $Q_{10}$  rises again. So, the  $Q_{10}$ -dynamics is a result of the changing amount of decomposable matter in the different temperature treatments. In the literature, it is sometimes not reported when the respiration measurement for the  $Q_{10}$ -determination was made, which makes an intercomparison difficult (e.g. Dutzler-Franz, 1981; Schinner and Gstraunthaler, 1981). If the different studies used in the literature review by Kirschbaum (1995) had used different incubation times for the calculation of  $Q_{10}$ s, the  $Q_{10}$ -dynamic with incubation time may also have been a source of variance in that literature review, where there was a decent scatter in the non-linear regression between  $Q_{10}$  and incubation temperature.

We conclude, that it may not be admissible to

derive the  $Q_{10}$  of C-mineralisation from the respiration rates at only one arbitrary incubation time, because then the temperature effect is confused with the incubation-time effect. There are three ways to solve this problem: (1) calculate the  $Q_{10}$ -values from only the respiration rates at the beginning of the incubation (e.g. Winkler et al., 1996), because the composition of the samples is still unaltered. (2) use the respiration rates at a very late incubation time (e.g. Ross and Cairns, 1978), when the light fraction is (nearly) mineralised and respiration rates are nearly constant. (3) fit a model of carbon mineralisation combined with a temperature response function of the rate constants to the mineralisation curves.

With approaches 1 and 2 only a small part of a long-term incubation is considered. Moreover, at the beginning of an incubation, soil respiration may still be influenced by disturbance, introduced by sample preparation (e.g. Blet-Charaudeau et al., 1990; Schinner et al., 1993), while at the end of an incubation inhibiting metabolites may have accumulated, which could adulterate the temperature dependence of C-mineralisation (c.f. Kirschbaum, 1995). Therefore, we strongly suggest to fit a model of carbon mineralisation combined with a temperature response function of rate constants to the temperature-dependent mineralisation curves as done, e.g. in this and several other studies (e.g. Updegraff et al., 1995; Lomander et al., 1998; Kätterer et al., 1998). This approach provides the temperature dependence of decomposition rate constants, and, additionally, the model is compatible with current carbon balance models (Parton et al., 1987; Andrén and Kätterer, 1997), which also use temperature-dependent rate constants.

In the future, also the effect of different carbon mineralisation models on the analysis of temperature dependence from experimental data should be investigated (e.g. single or two fraction first order decay, c.f. Andrén and Paustian, 1987; Q-model of Ågren and Bosatta, 1996). Further, it should be assessed if all or-

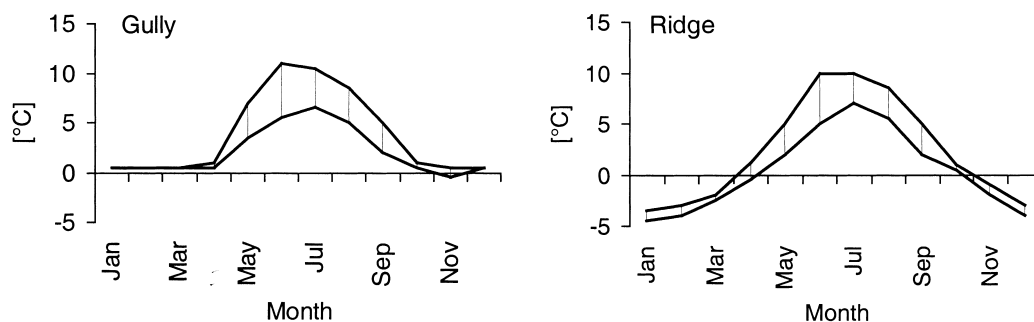


Fig. 3. Annual time course of monthly mean of daily maximum (upper curve) and minimum (lower curve) temperatures in soil at 5 cm depth, for gully and ridge (measured data extracted from Turner et al. (1975)).



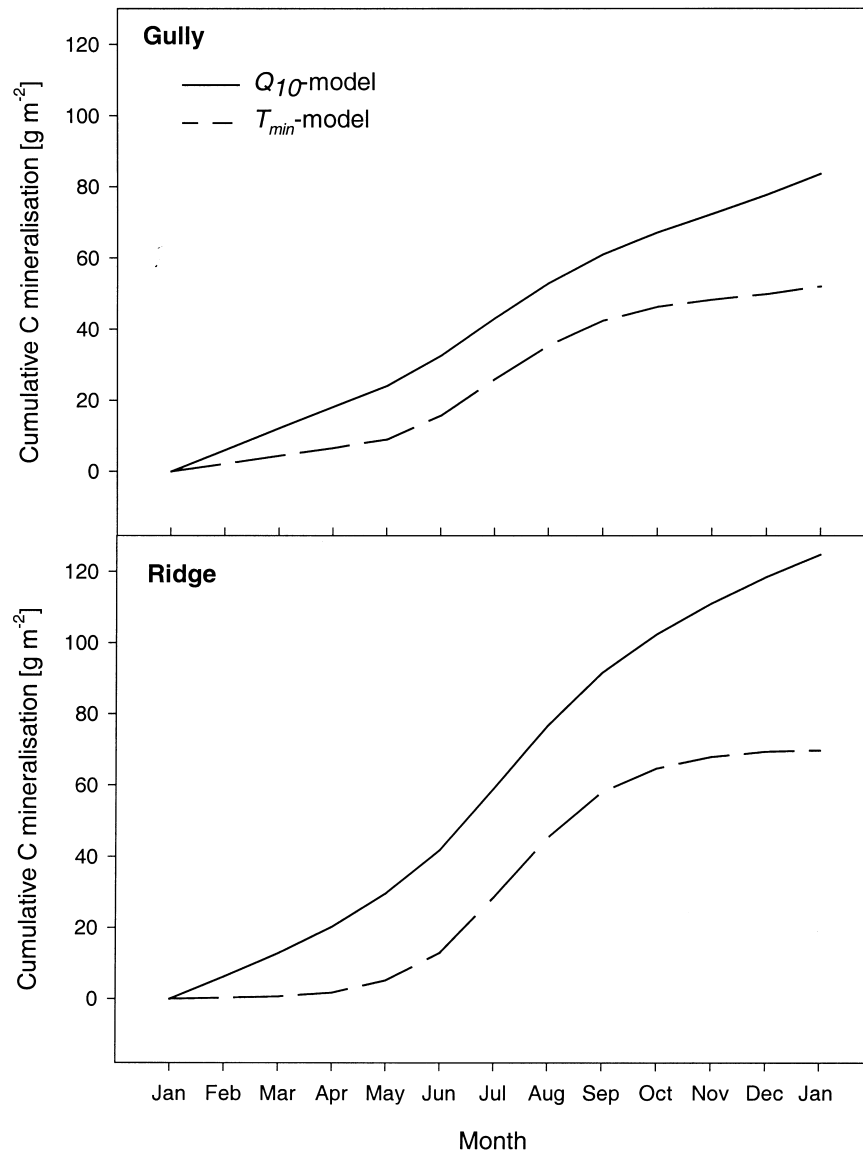


Fig. 4. Annual course of cumulative modelled C-mineralisation from the A-horizon of the gully and the Oe/Oa-horizons of the ridge, predicted by models using different temperature response functions.

ganic matter fractions are equally affected by temperature. For example, Bunnell et al. (1977a, 1977b) found a higher  $Q_{10}$  for ethanol-soluble substances than for non-soluble substances, and also Anderson (1991) reported different temperature dependencies for the decay of different soil organic matter fractions. At least one mineralisation model is available, in which different temperature dependence for litter and mineral soil are assumed (Rodrigo et al., 1997). On the other hand, Kätterer et al. (1998) did not find important differences between the temperature responses of the decomposition rate constants  $k_1$  and  $k_2$ , when they analysed 25 incubation time series taken from the literature, allowing  $k_1$  and  $k_2$  to vary independently of each other.

#### 4.2. Extrapolation to the field

Our area-based calculations of carbon mineralisation in the field were contingent both, on the estimates of carbon storage in the field and on rate constants estimated in the laboratory. Despite the high spatial variability of soil carbon storage, it had been estimated quite exact for the organic layer at the ridge site (Bednorz et al., 2000). However, by taking disturbed samples, the mineralisation rates can be enhanced or reduced (Cabrera and Kissel, 1988; Hokkanen and Silvola, 1993; Schinner et al., 1993; Oberholzer et al., 1996; Lomander et al., 1998). Thus, the rate constants may have been over- or underestimated. We showed here that the temperature response of decomposition

also introduces uncertainty, since the predicted decomposition rates differed considerably among the different temperature response functions. This uncertainty of around 30% concerning annual carbon fluxes associated with the temperature function is quite remarkable as it contrasts the laboratory study, where both functions gave very similar fits (e.g.  $R$ -squares). Considering that well-known generic soil organic matter decomposition models differ in their temperature response functions much more than the two functions we used, (with  $Q_{10}$ s varying from 1.9–3.0, Rodrigo et al., 1997), this point gets even more importance. Thus, model predictions of carbon balances, especially for cool-climate biomes, should be interpreted with caution, when the model was not newly calibrated.

Recognising the above mentioned uncertainties in ICBM-model parameterisation for our site, we present only a rough estimate of annual carbon mineralisation. However, these rough estimates of 52–84 g C m<sup>-2</sup> (gullies) and 70–125 g C m<sup>-2</sup> (ridges) annual carbon turnover are in the range of annual above-ground NPP at similar sites (48–220 g C m<sup>-2</sup> at Mt. Patscherkofel, Austria: Schmidt, 1977; 110 g C m<sup>-2</sup> at Niwot Ridge, Colorado, USA: Williams et al., 1998). Another assessment of the results can be made by comparing the estimated turnover times. Using a non-linear regression of turnover times against mean annual temperature, Johnson (1996) calculated a turnover time of 50 years for the organic layer of coniferous forests in North America, if mean annual temperature is around 0°C. For our site, Turner et al. (1975) published a mean annual temperature of 1.5°C, and we estimated a turnover time for the organic layer of the dwarf shrub heath of 46–80 years. These general agreements between other studies in comparable ecosystems and our findings are remarkable as we did not fit any parameter apart from the laboratory part. However, the mentioned uncertainties remain, and this does not mean any ‘validation’ of the up-scaling approach from the laboratory and our calibration, as calibration errors could have compensated each other (e.g., a too high  $h$  can be compensated by a too high  $k_2$ ). A validation with field observations would be necessary to clarify the above mentioned uncertainties, even though soil respiration measurement techniques in the field may also produce both, systematic and random errors (Rayment and Jarvis, 1997; Norman et al., 1997; Fang and Moncrieff, 1998).

The results concerning the seasonal contribution to the annual decomposition are more certain, as the relative contribution does not depend on the uncertain parameters ( $k_1$ ,  $k_2$  and  $h$ ), but only on the monthly  $r$ -factors and thus on the temperature response function. We can make the conservative estimate that a least 22% of annual C-mineralisation in the ridges occurred outside the growing season, and at least 40% (and

likely above 50%) in the gullies. Clein and Schimel (1995) expected 10–30% of annual mineralisation in tundra and boreal forests to take place during this period. Sommerfeld et al. (1993) computed (based on field measurements) a portion of 25% during winter. Our results support the view, that also wintertime decomposition has to be considered in carbon balance studies (Sommerfeld et al., 1993).

#### 4.3. Conclusions

Our study revealed the difficulties to compare studies regarding temperature response of soil carbon mineralisation even under laboratory conditions, and the necessity to standardise the method of analysis. We show that an approach combining a decomposition model with a temperature response function for the decomposition rate constant uses the full information of incubation time series and avoids the problem of a time dependent  $Q_{10}$ . A two-component decomposition model seems to be reasonable for most laboratory incubation studies.

Even though both temperature functions we applied yielded high  $R^2$ -values ( $>0.98$ ) in the laboratory study and gave very similar fits, the predicted annual carbon mineralisation in the field differed by more than 25% between the functions. This has to be considered when applying fitted functions from the laboratory to the field. Nevertheless, a simple up-scaling of soil carbon mineralisation rates from the laboratory to the field scale rendered realistic estimates of annual C-mineralisation, and we evidenced that decomposition outside the growing season cannot be neglected at our study site, but accounts for at least 22 or 40% of annual decomposition, on the ridges and the gullies, respectively.

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