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MODELLING THE EFFECTS OF TEMPERATURE AND MOISTURE ON CO_2 EVOLUTION FROM TOP- AND SUBSOIL USING A MULTI-COMPARTMENT APPROACH

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Summary—A novel approach, at least for laboratory conditions, for analysis of the dependence of soil C evolution on temperature is presented. A two-component (labile and refractory organic C) parallel first-order model was fitted to CO_2 evolution rates from top- and subsoil, incubated at different combinations of temperature (constant −4, 0.3, 5, 15, 25, weekly fluctuating between −4 and +5°C) and moisture (17, 26, 36 and 50% H_2O for the topsoil and 16, 23, 31 and 41% for the subsoil) and to the evolution of CO_2 after the addition of roots or stubble of *Phalaris arundinacea* in the topsoil, measured at 25°C and 36% H_2O (Lomander *et al.*, 1998). The size of the pools and their respective first-order rate constants were optimized simultaneously by a least-squares method. The optimization was carried out separately for top- and subsoil. Quadratic functions were fitted to the temperature and moisture responses. For topsoil samples in which roots or stubble were added, a three-component model (labile, refractory and stubble or roots) was used. The initial partitioning of the soil C, the decomposition rate constants for each partition and the temperature and moisture responses were all assumed to be identical to those of pure topsoil, while the initial pool sizes of added roots and straw were measured. The calculated temperature at which CO_2 evolution ceased (T_{min}) was −0.83°C, and a recalculation to Q_{10}-values resulted in increasing temperature response with decreasing temperature (Q_{10}=2.2 at 25°C and 12.7 at 0.3°C). Simulated CO_2 evolution rates agreed well with the measurements (R^2_{adj}=0.96 and 0.81) for top- and subsoil, respectively. The multi-compartment approach was superior to the single-compartment approach, which gave R^2_{adj}=0.88 and 0.76 for top- and subsoil, respectively. In general, CO_2 evolution rates obtained from the laboratory experiment were higher than those measured in the field, even after differences in temperature and moisture were taken into account. After 300 d in the laboratory at 25°C and 36% H_2O, 99% and 86% of the added straw and roots, respectively, had disappeared according to the described model. The CO_2-evolution rate per unit of soil carbon was about two times higher for topsoil than for subsoil. © 1998 Elsevier Science Ltd. All rights reserved

INTRODUCTION

The dependence of decomposition rates on temperature is usually described by the Q_{10}-function, an expansion of the Arrhenius function (e.g. Jørgensen, 1994), but other responses have also been used (e.g. Honeycutt *et al.*, 1988; Lloyd and Taylor, 1994). Ecosystem process models which attempt to model the seasonal cycle of terrestrial gas exchange have traditionally used a Q_{10} value (the factor by which the activity is increased when the temperature increases by 10°C) near 2 (Raich *et al.*, 1991). However, considerable differences in Q_{10} values may occur between different temperature intervals (Kirschbaum, 1995), and temperature response can often be better described by other functions. For example a quadratic function to model the temperature response was fitted to experimental data by Ratkowsky *et al.* (1982). This function, originally developed to describe the temperature dependence of microbial growth in pure cultures, was shown to be valid for a range of soil microbial communities as well (Díaz-Raviña *et al.*, 1994). Moisture response is often described as a log-linear function of soil water potential (see e.g., Orchard and Cook, 1983; Andrén and Paustian, 1987; Andrén *et al.*, 1993), but quadratic or other functions have also been proposed (Cassman and Munns, 1980; Myers *et al.*, 1982; Howard and Howard, 1993).

According to pertinent literature, the observed rates of C mineralization are heavily influenced by the pre-treatment of the soil before measurements (Beauchamp *et al.*, 1986), soil type (Howard and Howard, 1993) and the prevailing climate at the site of the soil (Anderson, 1991). There are no general

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models available which can be used to account for differences in all these factors. Therefore, there is a need for improved theoretical analysis, i.e. mathematical modelling, of the laboratory incubation data. Since few studies have been carried out on cold and heavy soils, they are of special interest.

In this study, a data set comprising CO_2 evolution rates from a heavy clay soil incubated at different temperature and moisture regimes (Lomander *et al.*, 1998) were used. The main objective was to test if a multi-compartment modelling approach to analyze the temperature and moisture dependence of soil C evolution is superior to the commonly used single-component approach. Further, results from the laboratory incubations were compared with measurements and model outputs from field investigations on the same soil as that used in this study (Andrén *et al.*, 1996; Kätterer and Andrén, 1996).

MATERIALS AND METHODS

Site description and sample preparation

Topsoil (0–25 cm) and subsoil (30–55 cm) samples were taken from four conventionally fertilized plots, cropped with reed canarygrass (*Phalaris arundinacea* L.). The soil was classified by Andrén *et al.* (1990) as a Fluventic Eutrocrept (Limenthic, Soil Survey Staff, 1975). Mean clay content at 0–55 cm is about 53%.

The soil samples were crumbled into fragments (dia < 10 mm) and most of the roots and other visible organic material were removed. The water content was adjusted to four values between the wilting point and 100% WHC (17, 26, 36, 50 and 16, 23, 31, 41 g H_2O 100 g dry soil for top- and subsoil, respectively). Thereafter the soil samples were incubated at −4, 0.3, 5, 15, 25°C or weekly fluctuating −4/5. At one moisture and temperature combination (25°C, 36 g H_2O) 300 mg of roots or 300 mg of stubble were added to the soil before incubation. The treatments (50 total; i.e., 4 water contents × 6 temperatures × topsoil and subsoil = 48, plus "root" and "stubble" treatments) were replicated three times.

In the following text, topsoil samples (T) with added stubble (S) and roots (R) will be referred to as, i.e., TS 25/36 and TR 25/36, where the first value indicates the incubation temperature (°C) and the second indicates water content (%H_2O 100, dry soil mass basis). Correspondingly, subsoil samples will be referred to as A (from alv, the Swedish name for subsoil).

Soil respiration was measured as CO_2 evolution at increasing time intervals, i.e., from 1-week intervals at the beginning of the experiment to 4-week intervals after 6 months. Before analyzing in a gas chromatograph, CO_2 was accumulated by closing the incubation vessel for several hours. Further details regarding the soil and the experimental design, as well as a presentation and discussion of the results from the measurements of CO_2 evolution rates are presented by Lomander *et al.* (1998).

Carbon mineralization model

Carbon mineralization was assumed to proceed from independent pools of organic matter. Using a least-squares fitting procedure (procedure NLIN in SAS; SAS Institute Inc., 1982), a two- or three-component parallel first-order model was fitted to the measured CO_2 evolution rates (C_{flux}):

$$C_{\text{flux}} = \sum C_{\text{tot}} \alpha_i k_i f(T,w) \exp(-k_i f(T,w) t); \quad \sum \alpha_i = 1 \tag{1}$$

where t is time (days), C_{tot} is the total initial amount of carbon and α_i is the fraction of each of the assumed organic pools. The index i denotes labile and refractory organic C pools for two-component models, while for three-component models i denotes labile, refractory and either added straw (TS) or roots (TR). The corresponding decomposition rate constants are denominated k_i. The function $f(T, w)$ is a response function, and represents the modification of the rate constants for the effects of both temperature (T) and moisture (w).

$$f(T,w) = E_T E_w. \tag{2}$$

A quadratic function proposed by Ratkowsky *et al.* (1982) was used to describe the temperature response (E_T)

$$E_T = b^2 (T - T_{\min})^2 \tag{3}$$

and another quadratic function was used to describe the moisture response (E_w).

$$E_w = d_1 w^2 + d_2. \tag{4}$$

We assumed that no interaction between temperature and moisture occurred within the intervals used here (see results) and that the temperature and moisture response were equal for all organic fractions. Thus, where T is the incubation temperature, $T_{\min}$ is a hypothetical value at which the CO_2 evolution is zero and b is a constant. The mass of water g^{-1} dry soil, i.e. the gravimetric water content, is denoted w, while d_1 and d_2 are constants. E_T was normalized for 25°C:

$$b = \sqrt{1}/(25 - T_{\min})^2; \quad E_T(25) = 1. \tag{5}$$

Then, inserting equation (5) in equation (3) gives

$$E_T = (T - T_{\min})^2/(25 - T_{\min})^2 \tag{6}$$

E_w was normalized for the highest water content in the soil ($w_{\max}$; i.e., 50% and 41% for top- and subsoil, respectively), hence:

$$d_2 = 1 - d_1 w_{\max}^2; \quad E_w(w_{\max}) = 1. \tag{7}$$

Substituting d_2 in equation (4) with equation (7) gives:

$$E_w = 1 - d_1(w_{max}^2 - w^2). \quad (8)$$

First, the parameters for the fraction of labile organic material (α_l), the first-order rate constants (k_l and k_r) and the values for T_{min}, and d_1 were optimized simultaneously using equation (1). The data set consisted of three replicates, taken at 14 occasions, of each of the top- and subsoil samples having a CO_2 evolution rate significantly different from zero (topsoil samples with 17, 26, 36 and 50% H_2O incubated at 0.3, 5, 15 or 25°C, subsoil samples with 31 and 41% H_2O incubated at 5°C and subsoil samples with 16, 23, 31 and 41% H_2O at 15 or 25°C), for a total of 1092 measurements. Since CO_2-evolution rates in all subsoil treatments at 0.3°C and for the two lowest moisture contents at 5°C were not significantly different from zero, T_{min} was not estimated separately for the subsoil but was assumed to be the same as that estimated for the topsoil.

In a second step, three-component models were fitted to the measurements for the treatments TR and TS. The initial pool sizes of labile (α_l) and refractory (α_r) decomposable organic material and their respective decomposition rates (k_l, k_r) were assumed to be identical to those obtained for pure topsoil. The measured organic C in the added roots or stubble was used as the initial value for the third pool. The parameters T_{min} and d_1, were also assumed to be identical to those of the pure topsoil. Hence, the only parameter that was optimized for the treatments TR and TS was k_{TS} or k_{TR}, respectively.

Comparison with the field situation

Kätterer and Andrén (1996) used a simulation model to estimate C and N-mineralization in the field from the same soil that was used in our experiment. In that field application, the estimated amount of initial C mineralized from the topsoil in the treatment with the highest mineralization was about 50 g m^{-2}, which corresponds to 0.42% of the initial C stock. Under "constant-summer" conditions (optimal moisture and 20°C), about 1.1% would have been mineralized ($1 - \exp(-0.00003 \times 365) = 0.011$). Thus, decomposition in the field during that year proceeded at about 38% of its "constant-summer" rate (0.42/1.1). Since temperature dependence was modelled to follow a Q_{10} function with $Q_{10} = 2$ and 20°C as the reference temperature, we can roughly calculate a constant "mean temperature" which would result in the same actual C mineralization during that year, i.e., $0.38 = 2^{(T-20)/10)}$. Solving for T, the resulting "mean temperature", and thus the value of the response E_T in our model (equation (6)) was calculated. If we further assume the moisture conditions of 36% to be comparable with the prevailing field conditions (equation (8)), we can calculate the contributions from the topsoil to the total C mineralization according to equation (1) (cf. Table 1).

Model properties

A model experiment was performed in which organic material corresponding to 1 g C was assumed to decompose, of which 20 mg C is labile and 980 mg C is refractory. We assumed that the corresponding first-order decomposition rate constants were (multiplied by the climate response factor) 2 and 0.002% d^{-1} in one "warm" case and 50% of these values (0.01 and 0.00001% d^{-1}), respectively, in another "cool" case.

Statistical analysis

The fitting of the models and the calculation of the coefficients of determination adjusted for the number of model parameters (R^2_{adj}) were made using the SAS procedures NLIN and REG (SAS Institute Inc., 1982). For more detailed descriptions of the statistical analysis, see Lomander *et al.* (1998).

RESULTS

Initial total amounts of organic carbon, as well as optimized parameter values for the treatments are given in Table 1. The obtained value of T_{min} for the topsoil was –0.83°C, i.e., modelled CO_2 evolution ceased at this temperature (Table 1). A recal-

Table 1. Initial amounts of organic C in top- and subsoil as well as in added roots and stubble (mg g $soil^{-1}$) and C-evolution rates (k_i; % day^{-1}) from three components (α_i; % of initial amount), where index l, r and TR/TS refers to the labile, refractory and root/stubble pool, respectively. Parameters d_1 and T_{min} refer to moisture and temperature response functions (equations (6) and (8))

	Pure topsoil	Topsoil + roots	Topsoil + stubble	Subsoil
Total initial C	23.7	23.7 + 1.6	23.7 + 1.7	13.1
α_l	0.24	0.22	0.22	0.074
α_r	0.76	0.71	0.71	0.93
$\alpha_{TR/TS}$	0.064	0.068		
k_l	0.796	*	*	0.552
k_r	0.0394	*	*	0.0196
$k_{TR/TS}$		1.31	3.59	
d_1	4.19	*	*	5.64
T_{min}	–0.83	*	*	*

*Value set to that for pure topsoil.

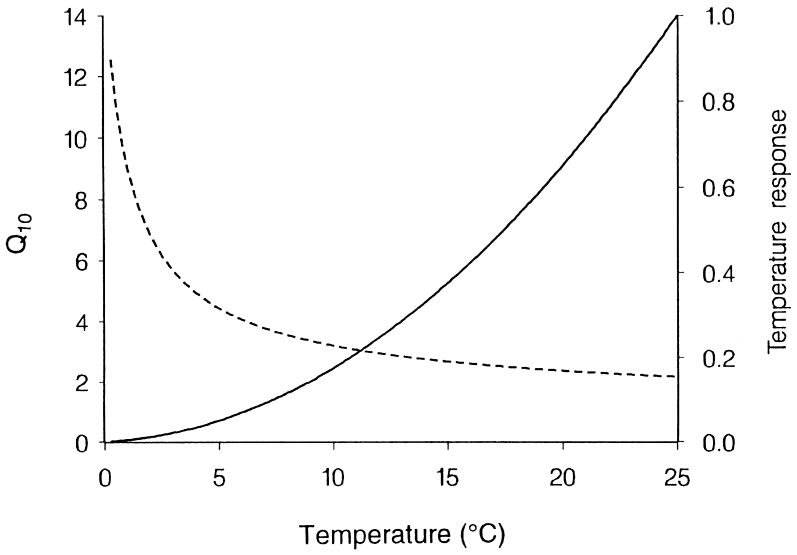

Fig. 1. The response of CO_2 evolution to temperature, calculated by fitting equation (1) to CO_2 evolution data from the topsoil incubations. Q_{10}-values (- - -) were calculated after first fitting the function by Ratkowsky *et al.* (1982) (———).

culation of the temperature response to Q_{10}-values ($T_{ref} = 25°C$) showed that Q_{10} increased with decreasing temperature; from 2.2 at 25°C, to about 12.8 at 0.3°C (Fig. 1). Since the CO_2 evolution rates at lower temperatures in the subsoil were not significantly different from zero, there were not enough data to optimize a separate temperature response and therefore T_{min} was assumed to be the same as for the topsoil (Table 1).

Decomposition rates of the labile and refractory fractions were about 1.3 and 2.0 times higher, respectively, in the topsoil than in the subsoil (Table 1). Stubble (3.59% d^{-1}) decomposed about three times faster than did roots (1.31% d^{-1}).

According to the model, the stubble and roots had decomposed almost completely (99 and 86%, respectively) after 300 d and the labile pool had decreased with 70% in the topsoil, and 62% in the subsoil. This is equivalent to a decrease in the total amount of organic C with about 21% for T 25/36, 26% for TR 25/36 and TS 25/36 and with about 8% for A 25/31.

To illustrate the combined effect of temperature and moisture on CO_2 evolution rates, three-dimensional response surfaces (Fig. 2) were constructed for the modelled product of the temperature (equation (6)) and moisture response (equation (8); see Table 1 for parameter values). Note that since neither the temperature (equation (6)) nor the moisture response (equation (8)) is linear, the response surface is curved in two dimensions. The bowl-shaped form of the surface is shallow, however, since the quadratic function can almost be approximated with a linear function. At the lowest temperatures, no activity can be seen, regardless of moisture content. However, at the lowest moisture, the activity is increasing with increasing temperature.

Different combinations of temperature and moisture response functions, as well as a single-compartment model were fitted to the CO_2 evolution rates. Both a Q_{10}-based model ($R^2_{adj} = 0.94$ and 0.78 for top- and subsoil) and a power temperature response function ($R^2_{adj} = 0.95$ and 0.80 for top- and subsoil), as well as a log/linear ($R^2_{adj} = 0.90$ and 0.77 for top- and subsoil) and a linear moisture response ($R^2_{adj} = 0.94$ and 0.79 for top- and subsoil) resulted in lower coefficients of determination than the temperature (equation (6)) and moisture responses (equation (8)) used in our model ($R^2_{adj} = 0.96$ and $R^2_{adj} = 0.81$ for top- and subsoil, respectively; Fig. 3). Fitting a single-compartment model (quadratic temperature and moisture response) also resulted in lower coefficients of determination ($R^2_{adj} = 0.88$ and 0.76 for top- and subsoil, respectively).

The estimated "mean temperature" under field conditions (see Section 2) was 6.04°C, which according to our model (equation (6)) gave the temperature response $E_T = 0.071$. The assumed field moisture conditions (36%) gave E_w(topsoil) = 0.50 (equation (8)). According to our experiment (equation (1)), about 2.7% of the initial C amount would evolve from the topsoil under field conditions, according to our experiment. Thus, extrapolation of results from our study to the field would result in a 6-fold overestimation of the CO_2 evolution.

According to the model experiment (described in Section 2), the labile substrate was more rapidly depleted in the "warm" treatment. Consequently,

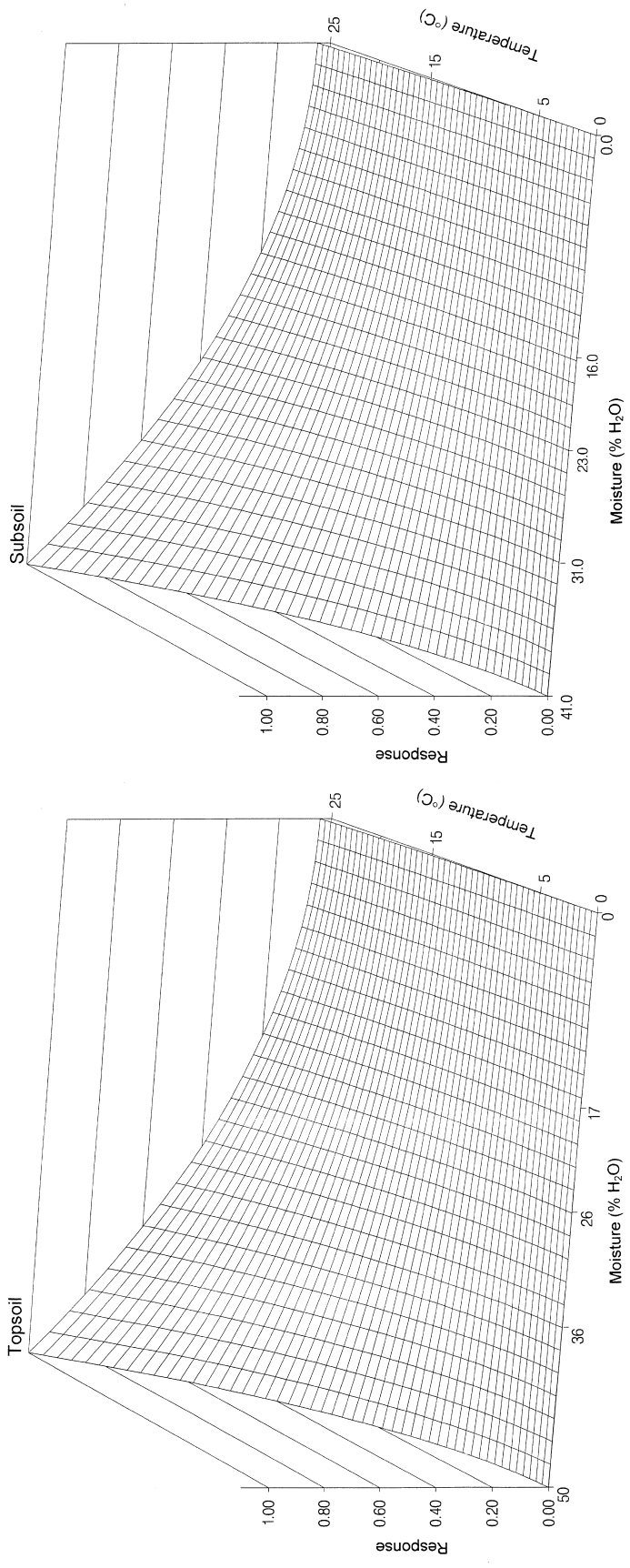

Fig. 2. The modelled response of CO_2 evolution (the product of equations (6) and (8)) to temperature and moisture

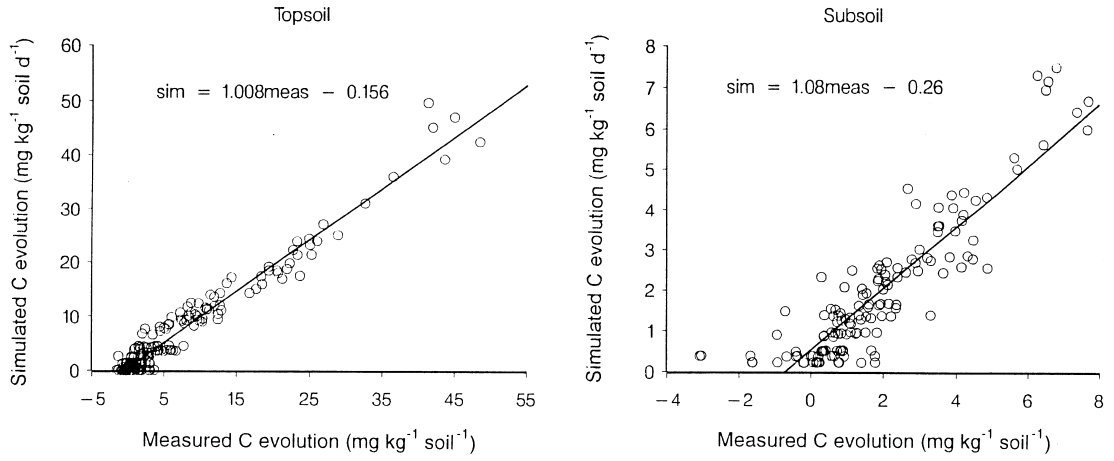

Fig. 3. Simulated C evolution rates (sim) from top- and subsoil as a function of measured C flow rates (meas) in top and subsoil

rates became relatively higher in the "cold" treatment where a substantial amount of easily available substrate remained. Under certain conditions, ($80 > t < 280$; Fig. 4) rates in the "cold" treatment even exceeded those in the "warm" treatment.

DISCUSSION

The main advantages of using a dynamic multi-compartment model to analyze temperature responses are: (1) the entire datasets can be used for the analysis, and (2) changes in rates with respect to time can be handled accurately. A two-compartment model is probably sufficient to describe C evolution from soil during short-term incubation in most cases. However, the single-compartment approach that has been used almost exclusively for analysis of soil incubations in the laboratory (Jenny *et al.*, 1949; Howard and Howard, 1974) is not sufficient for such a description. Winkler *et al.* (1996), for example, calculated Q_{10}-values for respiration of a forest soil. They used the initial rates of respiration from the A-horizon brought into the laboratory and estimated Q_{10}-values to vary between 1.7 and 1.9 over a temperature range from 4°C to 28°C. A recalculation of their data using our model resulted in higher Q_{10}-values (2.46) at lower temperatures and lower Q_{10}-values (1.65) at higher temperatures. Nevertheless, their approach only using initial rates is probably more appropriate than

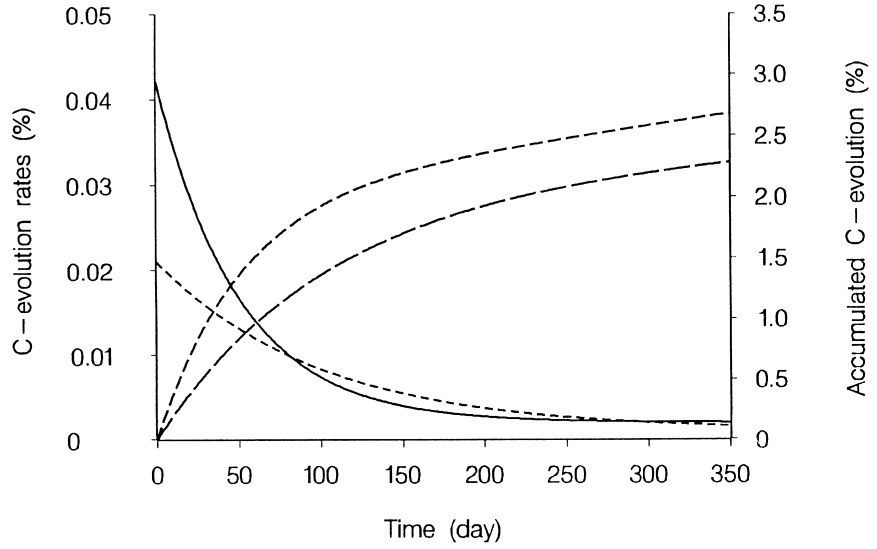

Fig. 4. C evolution rates (———; —— ——) and accumulated values (· · ·; - - -) for a model experiment using (equation (1)). Rate constants ($k_1 = 2\%$ day^{-1} and $k_2 = 0.002\%$ day^{-1}) and initial partitioning into the corresponding pools ($\alpha_1 = 0.02$ and $\alpha_2 = 0.98$) were equal in both cases. The value of the climate-related function ($f(T, w)$) was 1.0 and 0.5, respectively

using rates obtained at later days or using accumulated C evolution to calculate Q_{10}-values (see discussion below). However, the calculated responses using only initial rates are sensitive to the precision of a measurement on one single day, with the information gained from the rest of the incubation being simply discarded.

Furthermore, using rates for calculating, temperature responses will depend on the time selected for the analysis (Fig. 4). Hunt (1977) pointed out the risk for substrate depletion, i.e., exhaustion of readily-available substrates under conditions favorable for microbial activity, but not under less favorable conditions. Our approach can account for the temporal changes in substrate availability without affecting the response to temperature or moisture.

Allocation of initial carbon (α_i) was highly correlated ($R > 0.95$) with the rate constants k_i (i = r, l), and the rate constants were highly correlated with each other. However, correlation between α_i, k_i and the parameters determining moisture and temperature responses (d_1 and $T_{\min}$) was low ($R < 0.16$). This implies that changes in α are compensated for by changes in k_i and vice versa without affecting the fit of the model, but that the temperature and moisture responses are affected only marginally by these changes. For example, a change of α from 0.30 to 0.05 affected d_1 by about 0.1% and $T_{\min}$ by less than 0.1°C.

Díaz-Raviña *et al.* (1994) showed that the quadratic function, originally developed by Ratkowsky *et al.* (1982) to explain temperature responses of microbial growth for pure bacterial cultures, also can be applied to predict microbial temperature responses in soil. $T_{\min}$ for the CO_2 evolution as estimated in our experiment was –0.83°C, which is considerably higher than those ($T_{\min} = -6$ and −10°C) estimated by Díaz-Raviña *et al.* (1994). This might be an indication of that our method underestimates the activity at lower temperatures.

The response of CO_2 evolution to temperature has been the focus of numerous experiments and has often been described by a Q_{10} relationship. An average Q_{10}-value of 2.4 for respiration studies has been suggested in a review by Raich and Schlesinger (1992) who compiled data from field experiments representing the world's major terrestrial biomes. The increase in Q_{10} with decreasing temperature ($Q_{10} = 2.2$ at 25°C and $Q_{10} = 12.8$ at 0.3°C) is in accordance with the data from Díaz-Raviña *et al.* (1994), and with Kirschbaum (1995), who combined literature data for C mineralization and found Q_{10}-values of 8 and even higher at 0°C. Due to the mathematical formulation of the Q_{10} function ($E_T = Q_{10}^{(T-T_{ref})/10}$, the activity becomes zero first when the temperature approaches negative infinity. Clearly, when temperatures are decreasing towards 0°C and activity approaches zero, the relative deviations between data and model become greater and greater, "forcing" extreme Q_{10}-values such as 8, 12 or even infinity.

Extrapolating the results from our experiment to the field conditions leads to an overestimation of C evolution by about a factor of 6. A corresponding comparison in the bare fallow treatment of the nearby Ultuna long-term experiment (Persson and Kirchmann, 1994; Andrén and Kätterer, 1997) resulted in overestimation of C mineralization from our laboratory investigation by a factor of 3.5.

The enhanced mineralization in the laboratory is almost certainly due to the pre-treatment. The digging out and partial homogenization of the soil can make larger surfaces available to microbial attack (Cabrera and Kissel, 1988). This response seems to increase with increasing clay content (Craswell and Waring, 1972). Another possible explanation of the relatively high CO_2 fluxes observed in our study may be the disintegration of carbonate. For example, Coleman *et al.* (1980) showed that between 30–60% of the released CO_2 from carbonate-rich soils is derived from carbonate.

An analysis of the remaining organic C in the soil after incubation was performed on three replicates of crumbled top- and subsoil, stored at +4°C and about 26% H_2O for 1.5 y. It showed that about 3.9% of organic C had disappeared from the topsoil, in comparison to the 1.4% calculated by applying the model based on CO_2 evolution for 1.5 y. The difference may seem large, but the precision of the analysis of organic C measurements was comparatively low (S.D. = ± 3.94%). The observed mean final organic C concentration was 2.21%, and the final concentration that would correspond to a 1.4% mass loss is about 2.27%. Thus, the two sets of measurements do not contradict each other.

The main purpose of our study was to model the influence of temperature and moisture on CO_2 evolution rates using a two-component parallel first-order model. However, the CO_2 evolution rates were high compared to a field situation and therefore extrapolation of these rates outside the laboratory may be questionable. Hokkanen and Silvola (1993) found that dependency of respiration measurements on temperature in intact soil cores differed slightly from those measured in the field. In our experiment, where measurements were performed on disturbed samples, an improvement could be to perform measurements on intact soil cores in the laboratory. The expected increase in variance as the samples would become more heterogeneous, could be handled by increasing the number of replicates.

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