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Aspects of carbon and nitrogen cycling in soils of the Bornhöved Lake district
II. Modelling the influence of temperature increase on soil respiration and organic carbon content in arable soils under different managements

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Abstract. Based on field measurements in two agricultural ecosystems, soil respiration and long-term response of soil organic carbon content (SOC) was modelled. The model predicts the influence of temperature increase as well as the effects of land-use over a period of thirty years in a northern German glacial moraine landscape. One of the fields carried a maize monoculture treated with cattle slurry in addition to mineral fertilizer ("maize monoculture"), the other was managed by crop rotation and recieved organic manure ("crop rotation"). The soils of both fields were classified as cambic Arenosols. The soil respiration was measured in the fields by means of the open dynamic inverted-box method and an infrared gas analyser. The mean annual soil respiration rates were 268 (maize monoculture) and 287 mg CO_2 m^{-2} h^{-1} (crop rotation). Factors controlling soil respiration were soil temperature, soil moisture, root respiration and carbon input into the soil. Q_{10}-values of soil respiration were generally higher in winter than in summer. This trend is interpreted as an adaptive response of the soil microbial communities. In the model a novel mathematical approach with variable Q_{10}-values as a result of temperature and moisture adjustment is proposed. With the calibrated model soil respiration and SOC were calculated for both fields and simulations over a period of thirty years were established. Simulations were based on (1) local climatic data, 1961 until 1990, and (2) a regional climate scenario for northern Germany with an average temperature increase of 2.1 K. Over the thirty years period with present climate conditions, the SOC pool under "crop rotation" was nearly stable due to the higher carbon inputs, whereas about 16 t C ha^{-1} were lost under "maize monoculture". Under global warming the mean annual soil respiration for both fields increased and SOC decreased by ca. 10 t C ha^{-1} under "crop rotation" and by more than 20 t C ha^{-1} under "maize monoculture". It was shown that overestimation of carbon losses in long-term prognoses can be avoided by including a Q_{10}-adjustment in soil respiration models.

Introduction

CO_2-exchange between atmosphere and ecosystems involves a flux from atmosphere to ecosystems, measurable as primary production, and an opposite flux, mainly due to respiration. A key question for climatic change research concerns a possible shift in the balance of these two fluxes under global warming. Such a shift may be very significant due to the large amount of carbon stored as soil organic matter. Whereas the effect of temperature on net primary production is well known, our knowledge about effects on respiratory processes, especially soil respiration is sparse.

Although there are other feedbacks between greenhouse gases in the atmosphere, climate and ecosystems, we focus here on the relations between elevated temperatures and soil organic carbon (SOC). Higher decomposition rates of soil organic matter caused by higher temperatures would increase the greenhouse gas CO_2 in the atmosphere: a so-called feedforward cycle. Though this hypothesis is generally accepted (Jenkinson et al. 1991; Kirschbaum 1995), it is not clear to what extent elevated temperatures increase the decomposition rate, and how soil biological systems adjust to a warmer environment. Kirschbaum (1995) reported, that different relative sensitivities of decomposition processes to temperature – expressed as Q_{10}-values – were observed at sites under different mean annual temperatures.

In this study we propose that short-term temporal changes in soil temperature and moisture cause seasonal changes in Q_{10}-values as a result of microbial adjustment. Our hypothesis is based on field measurements on two arable soils, and is used to formulate a model of soil respiration and the long-term response of SOC. Two different climate data sets were used to predict the influence of a 2.1 K temperature increase as well as the effects of different land-uses over a period of thirty years.

The fields

The research area is located in Schleswig-Holstein, northern Germany near the Baltic See. The hilly area with elevations up to 40 m a.s.l. includes agroecosystems, beech forest, alder forest, grassland and a lake. It measures about 5 km^2 including 1 km^2 of lake surface. The agroecosystems under consideration are a maize-monoculture with addition of cattle slurry plus mineral fertilizers and a crop rotation that recieved organic manure (1990: *Avena sativa* L. and *Sinapis alba* L. as intercropping, 1991: *Beta vulgaris L.*, 1991/92: *Secale cereale* L. and *Lolium multiflorum* L. as intercropping). The soils of both fields were classified as cambic Arenosols. (For details see Dilly et al., this issue)

Methods

Soil respiration was measured in the fields by the open dynamic inverted-box method (Humfeld 1930; Porka 1931) and an infrared gas analyser (for details see: Kutsch 1996). Comparable systems were used by Koepf (1953), Edwards & Sollins (1973) and Cropper et al. (1985). Measurements were taken in parallel with eight PVC boxes. Box size was 12.5 × 16 cm (200 cm^2) with a height of 14 cm. Ambient air continuously passed through each box with 1 l per minute and was directed to the gas analyser at least 3 times an hour. The boxes were fixed on aluminium frames, which remained in the soil during the whole growing season. To prevent influences of the measurement on the soil properties the boxes were moved to another frame after two or three days. Ten frames were located pairwise in every field. In the maize field where the plants grew in 70 cm distant rows the frames were placed in and between the rows to detect the root-induced spatial variabilty of soil respiration (see Rochette et al. 1991). Soil temperatures at 10 cm depth were measured by a PT 100 sensor at one plot in every field in 1990 and 1991, and between each chamber in 1992.

In total, 383 complete diurnal courses of soil respiration were measured during the years 1990–1992. Daily mean soil respiration rates and daily mean soil temperatures were estimated from the data for each diurnal course. Q_{10}-values were calculated for 75 diurnal courses in 1992 by fitting the data to an exponential function. Mean Q_{10}-values were built for each measuring campaign lasting 10 to 14 days. Significance of the differences between the mean Q_{10}-values were tested by a *t*-test, or, if normality was not fulfilled, by a Mann-Whitney Rank Sum test. Soil moisture in the field was calculated with a calibrated model by Hoffmann (1993).

Results and preliminary discussion

Soil temperature turned out to be the main factor controlling soil respiration (Figure 1). The diurnal curve of soil respiration closely resembled that of the soil temperature at a depth of 10 cm. The temperature sensivity of a process was expressed by a Q_{10}-value, which quantifies the increase of the process rate with temperature increase of 10 K. Biological systems usually have a Q_{10}-value between 2 and 3. In the investigated fields Q_{10}-values calculated from diurnal courses of soil respiration were higher in early spring and late autumn than in summer (Figure 2). In spite of highly variable Q_{10}-values particularly in April most seasonal mean Q_{10}-values differed significantly ($p < 0.05$), except for the two mean values in August and the increase between August and autumn. Higher Q_{10}-values during winter were also reported by Koepf

(1954). The increase of the Q_{10}-values between June and July 1992 occurred after a four-week drought period followed by rewetting. These data indicate that the soil microflora is a variable, adjustable system, which is sensitive to temperature and moisture. Its sensitivity to temperature may be controlled by secondary factors (Haber 1958) such as (1) soil moisture (Carlyle & Than 1988), (2) substrate quality and quantity, (3) extreme events like freeze-thaw-sequences (Wynn-Williams 1982) or drought and rewetting (Orchard & Cook 1983) and (4) in the sense of adjustment the temperature history of the system itself. Kirschbaum (1995) reported, that the greatest relative sensitivity of decomposition processes was observed at sites of low temperatures (up to a Q_{10}-value of 8 at locations with a mean annual temperature of 0 °C). Effects of substrate quality and quantity were not observed. Possible effects of the mentioned factors (2), (3) and (4) were tested with a data set of 75 diurnal courses of soil respiration and soil temperature measured in both fields during 1992. For the soil moisture content we took the daily mean value from Hoffmann's (1993) soil water model. Temperature history was defined as the sum of the daily mean temperature of the last 30 days. An increase in soil moisture content by more than 15% of field capacity within one day following a period with soil moisture contents below 60% field capacity was defined as an extreme event of drought and rewetting. Due to heterogeneity and the interdependence of the factors it was very difficult to develop a statistically clear, numerical interpretation of the variations in Q_{10}-values. Among single factors soil moisture yielded a higher correlation coefficient ($r^2 = 0.51$) than the temperature history ($r^2 = 0.33$) as shown in Figures 3a and 3b. However, a combination of the factors "extreme events" and "adjustment to temperature" according to Eqs. 7–10 (presented in the next chapter) better explained the variations in Q_{10}-values ($r^2 = 0.63$; Figure 3c). These observations support our hypothesis that the seasonal differences in short-term temperature sensitivity reflect an adjustment of the soil microflora to temperature and moisture history. The adjustment of the soil microflora can be the result of both, changes in the physiology of particular species and of changes of species composition.

Other factors that control soil respiration over periods longer than a diurnal course are soil moisture, carbon input into the soil, and root respiration. The latter is species-specific and controlled by the phenology. In the maize monoculture the soil respiration was higher in the rows than in between them. The maximum differences were measured in July (Table 1). They indicate that roots contributed to soil respiration by at least 40%. However, considering the presence of roots also in the "interrows" (Tardieu 1988) we might assume a higher root respiration.

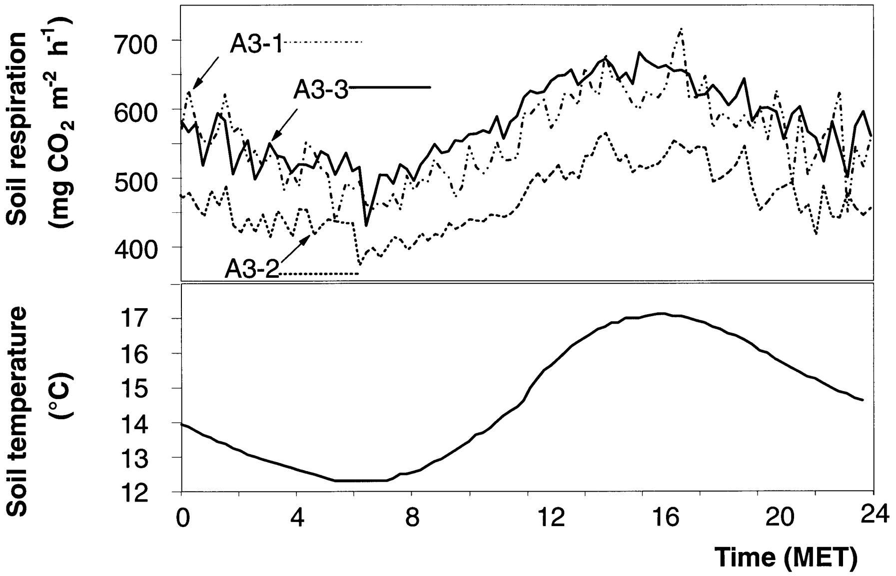

Figure 1. Diurnal courses of soil respiration and soil temperature at three sites of the field crop rotation. A3-1, A3-2, and A3-3 designate replicated plots.

Table 1. Maximum differences of soil respiration rates measured in the plant rows and in the space between the rows (interrows) of the maize monoculture field for the years 1990–1992.

Year	Maximum difference measured at date	Daily means of soil respiration (mg CO_2 m^{-2} h^{-1})		Least root respiration $\frac{(1)-(2)}{(1)} \cdot 100$
		Rows (1)	Interrows (2)	
1990	17.7.90	628	372	40.80
1991	23.7.91	1061	642	39.50
1992	17.7.92	750	414	44.80

The mean annual soil respiration rate was calculated from the field data as 268 (maize monoculture) and 287 mg CO_2 m^{-2} h^{-1} (crop rotation). The similarity between the rates of the two fields confirms the observations of Dilly et al. (this issue), who measured equal basal respiration of soil samples from both fields, although the microbial biomass was different. Krzysch (1964) calculated values between 280 and 400 mg CO_2 m^{-2} h^{-1} for soils under sugar beet. 270 mg CO_2 m^{-2} h^{-1} was obtained by Buyanowsky et al. (1986) for a field with winter wheat.

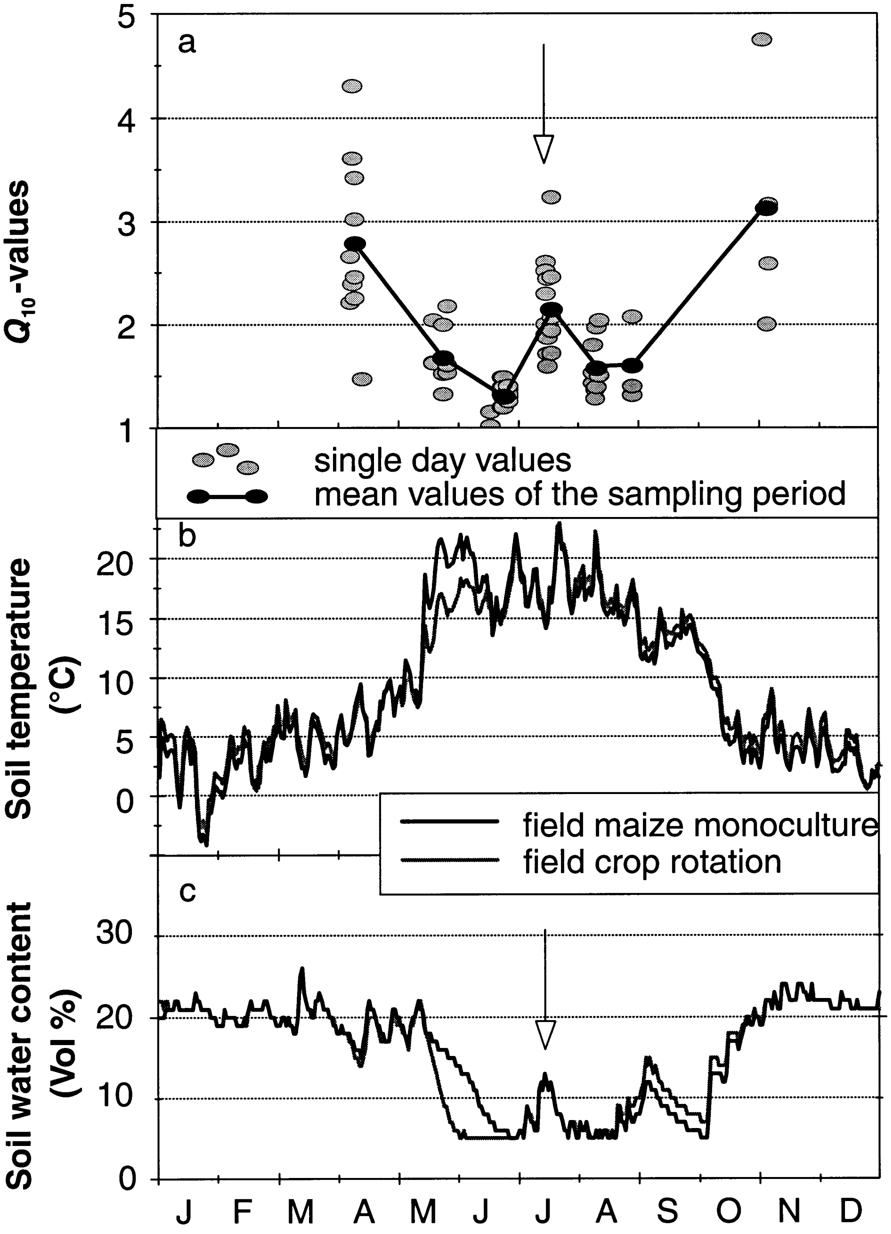

Figure 2. a: Seasonal variations of the Q_{10}-values derived from daily courses of soil respiration in both fields in 1992. Grey points are single values, black points an averages for each sampling period. The arrow marks an increase of soil moisture after a drought period. b: Annual course of soil temperature measured at 10 cm depth. c: Annual course of soil moisture at 10 cm depth (model output by Hoffmann, 1993).

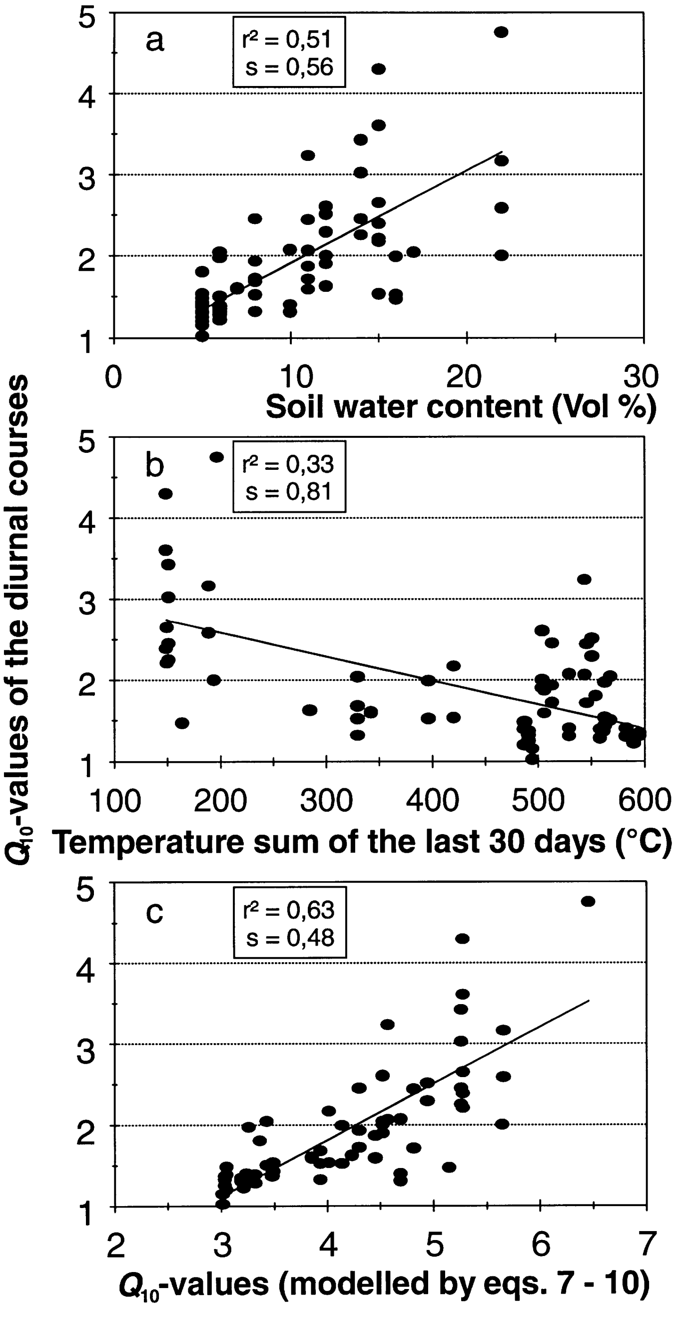

Figure 3. a: Regression between soil moisture and Q_{10}-values. b: Regression between temperature sum of the last 30 days passed before each measurement and Q_{10}-values. c: Regression between Q_{10}-values modelled by means of eqs. 7–10 and Q_{10}-values measured in the field.

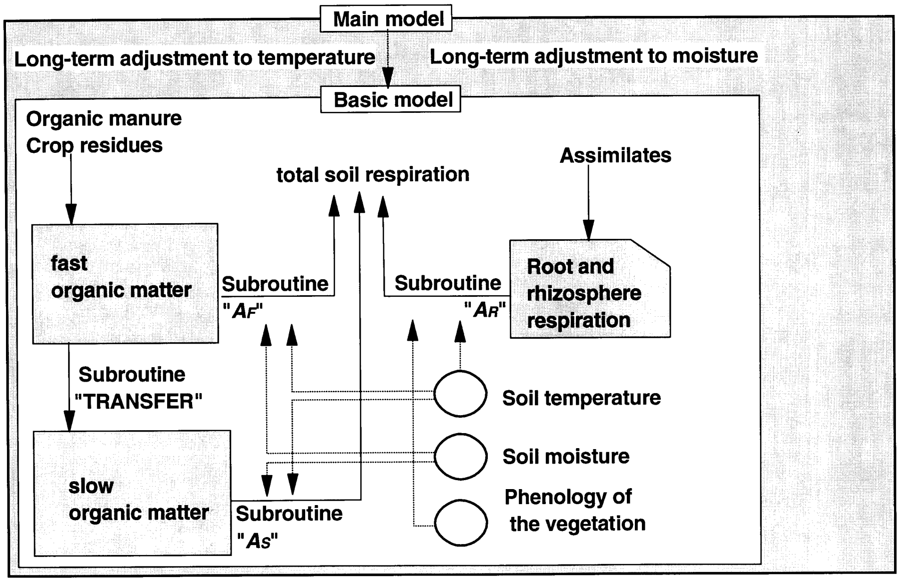

Figure 4. Structure of the two-tiered model accounting for long-term adjustment of soil respiration to changes in soil temperature and soil moisture.

Modelling

Most soil respiration models operate with a constant Q_{10}-value. The challenge which arises from our observations is the development of a model, which depicts the history of the system and its way of adjustment. For this purpose we developed a two-tiered model. The mathematical description of the actual response of soil respiration to temperature, moisture and carbon input forms the “basic model”. A “main model” on a higher hierarchical level controls the basic model by varying coefficients of the basic model as an expression of adjustment of the system (Figure 4).

Carbon dioxide is produced in soils by three processes: root and rhizosphere respiration (A_R) and respiration of fast and slow organic matter fractions (A_F and A_S respectively).

$$A = A_R + A_F + A_S \tag{1}$$

Root and rhizosphere respiration is driven by the plant and modified by temperature (T).

$$A_R = A_R^0 \eta f(T) \tag{2}$$

where A_R^0 is maximum root and rhizophere respiration, η increases smoothly from 0 to 1 between germination and flowering and declines thereafter (representing root growth followed by senescence), and *f*(*T*) is a function of temperature.

Respiration of fast and slow organic matter fractions is a first-order reaction with rate constants modified by soil water content (Θ) and temperature.

$$\begin{aligned} A_F &= k_F C_F f(\Theta) f(T) && (3) \\ A_S &= k_S C_S f(\Theta) f(T) && (4) \end{aligned}$$

C_F and C_S are concentrations (kg C ha^{-1}); k$_F$ and k$_S$ rate constants (d^{-1}).

Some of the fast pool is transformed to slow-pool SOM by a first-order reaction assumed to be unaffected by water and temperature.

$$J_{FS} = k_{FS} C_F \tag{5}$$

The water content function *f*(Θ) is a sigmoid reaching a maximum of 1 at Θ_c.

$$f(\Theta) = \frac{\exp\left[\left(\frac{\Theta}{\Theta_c} - 1\right)^{\alpha}\right]}{\left[\frac{(\Theta - \Theta_c}{\beta} + 1\right]^{\alpha}} \tag{6}$$

where α and β are empirical fitting parameters and Θ is the actual soil water content.

The soil temperature function *f*(*T*) is

$$f(T) = [\exp(aT - b)]^c \tag{7}$$

where

$$c = c_T + c_{DR} \tag{8}$$

$$c_T = \frac{m - \sum_{t-30}^{t-1}(T)}{n} \tag{9}$$

$$c_{DR}^{t} = c_{DR}^{t-1} + \omega - r c_{DR}^{t-1} \tag{10}$$

a, *b*, *m* and *n* are fitted parameters; ω equals 0 unless Θ^{t-1} is less than a critical value θ_c (taken here to be equal to 60% field capacity) and Θ^t exceeds Θ^{t-1} by at least 0.25 Θ_c, in which case ω is equal to 0.3; *r* is an empirically determined recovery coefficient.

The temperature function *f*(*T*) reflects the adjustment of the system to a different temperature regime through the running 30-day T-sum (c_T) and to drying and rewetting (c_{DR}). Parameter *c* in turn dictates the sensitivity of the system to short-term temperature variations.

The model runs in daily steps (t) with an input of daily mean soil temperature and soil moisture at 10 cm depth. Carbon is added to the fast organic matter fraction by manure and as plant residues after harvesting. Model output is the daily mean soil respiration and the soil organic carbon content.

Calibration of the model

The model was calibrated in two steps. First best-fit values of the parameters a, b, m, n, ω and r were produced by optimizing the Q_{10}-values of the model against 75 Q_{10}-values measured during the year 1992 in both fields (Figure 3c). As an effect of temporal integration the model reveals higher Q_{10}-values than the diurnal courses. Secondly, k_F, k_S, k_{FS}, α, and β were fitted using 221 daily mean values of soil respiration measured in the crop rotation field and 162 means measured in the maize monoculture field during the three years of field measurements. For both steps we used a least sum of squares procedure. The parameters were varied systematically in pre-chosen intervals, until s was minimized which was estimated after Kreyszik (1982):

$$s = \sqrt{\frac{\sum_{j=1}^{n}(v_j^{mod} - v_j^{mes})^2}{n-1}} \qquad (11)$$

in which v_j^{mod} is the modelled, and v_j^{mes} is the measured value.

Following Hansen et al. (1990) we used values between 0.001 und 0.005 d^{-1} for k_F and around 10^{-5} for k_S. A_R^0 was estimated empirically from the field data comparing plots with and without vegetation in the crop rotation field (1990) or were taken from the literature (Monteith et al. 1964; Biscoe et al. 1975; Hall et al. 1990). In the maize monoculture field A_R^0 was estimated by the difference between the rows and the interrows. As was discussed before the root respiration was higher than this difference. Therefore the field data between the rows were fitted against the model data of microbial respiration (A_R + A_F in eq. 1) plus 25% of the value computed for the root respiration (A_R in eq.1). The latter was done with data for July and August when the root system was fully developed and root activity highest. Best-fit values are shown in Table 2. The data of the maize monoculture field were fitted by the model very well ($r^2 = 0.88$). The correlation coefficient for the crop rotation field was much lower ($r^2 = 0.26$), possibly as a result of greater spatial heterogeneity.

To show the effect of the Q_{10}-adjustment in the model we also ran the basic model with a constant Q_{10}-value. The regression coefficients, the slopes of the regression line, and the standard errors for both model types are shown in Table 3. The monthly means of the differences between measured and

Table 2. Model parameters.

Parameter	Unit	Maize monoculture	Crop rotation
a	$°C^{-1}$	6.10	5.13
b	–	0.85	0.96
m	°C	1479	1180
n	$°C^{-1}$	1248	1210
ω	–	0.3	0.25
r	–	12	34
k_F^{-1}	d	965	576
k_S^{-1}	d	24950	21533
k_{FS}^{-1}	d	510	319
α	–	0.25	0.36
β	$\% FC^{-2}$	1000	1000

Table 3. Statistical quality of the models.

Parameter	Unit	Maize monoculture		Crop rotation	
		Variable Q_{10}	Constant Q_{10}	Variable Q_{10}	Constant Q_{10}
r^2	–	0.88	0.92	0.26	0.23
Slope	–	0.93	0.92	0.90	0.86
s (relative)	%	22.50	21.50	33.10	32.80
s (absolute)	mg CO_2 m^{-2} h^{-1}	94	81	115	125

modelled soil respiration shows Table 4. Although not all statistical values are supportive, the performance in the seasonal course is better described by applying an adjusted Q_{10}-value. Both models underestimate the apparent soil respiration in spring and autumn. In months of extreme soil drought (June for crop rotation and August for maize monoculture) an overestimation occurs, but in most cases the deviations from the measured values were smaller if modelled with the adjustment effect.

Simulation with a local GC-model

The calibrated model was used to estimate the impact of global warming with respect to different types of agricultural management. The model assumptions for carbon input (Table 5) were based on the long-term management of both fields. They do not exactly reflect the actual management of both fields, because recently (1991 and 1993) the farmer also treated the maize

Table 4. Monthly means of the deviations between modelled and measured soil respiration (% of measured) for both models and both fields (positive values indicate overestimation and negative underestimation by the model).

Month	Maize monoculture		Crop rotation	
	Variable Q_{10}	Constant Q_{10}	Variable Q_{10}	Constant Q_{10}
1	–	–	–	–
2	–	–	–	–
3	–	–	−3.10	−20.60
4	−47.50	−55.90	−11.90	−15.70
5	−4.00	−14.80	−5.20	−13.20
6	−2.90	−3.20	20.30	23.80
7	−6.40	−8.30	−0.20	−12.70
8	9.50	15.30	−2.90	−1.80
9	1.80	1.30	1.70	−1.10
10	5.00	−5.90	–	–
11	−4.50	−8.90	−27.20	−30.50
12	1.10	12.00	–	–

monoculture field with organic manure. In the model assumptions manuring and intercropping caused a mean annual carbon input to the soil of about 5 t per hectare per year in the field crop rotation, whereas the field maize monoculure recieved only 3.6 tons, mostly as plant residues.

For the investigation of the impact of a temperature increase two data sets generated by Hollwurtel & Beinhauer (1995) were available . So called "present-time" data were the climate data measured by the German Weather Service in Hamburg-Fuhlsbüttel for the 30 years period 1961 to 1990. Following Cubasch et al. (1992) in the data set of the "global warming scenario" an average temperature increase of 2.1 K and a constant mean annual precipitation was assumed. To generate the "global warming scenario" they searched in the "present-time" data for periods of the same weather situation in the similar season with higher temperatures and the same precipitation. The assembling algorithm handled air temperature with a higher priority than precipitation which had the consequence that long-term mean precipitation in July was 55 mm instead of 83 mm in and August 56 mm instead of 70 mm. The mean annual precipitation remained unaffected.

The monthly means of soil temperature and soil moisture at a depth of 10 cm are depicted in Figure 5 for both data sets. The "global warming scenario" reveals higher soil temperatures and a decrease of soil moisture. The mean Q_{10}-value (Figure 6), which was adjusted to the temperature sum of last 30 days and to drought and rewetting, was increased in winter and decreased in summer. Sudden increases of the Q_{10}-values after drought and rewetting did

Table 5. Model assumptions.

Crop rotation	Carbon input (kg C ha^{-1})	Maize monoculture	Carbon input (kg C ha^{-1})
		In the first year	
Organic manure	3300	Cattle slurry	1200
Plant residues	1500	Plant residues	2400
(spring cereal		(maize)	
Intercropping	500		
		In the second year	
Organic manure	3600	Cattle slurry	1200
Plant residues	1000	Plant residues	2400
(root vegetable)		(maize)	
Organic manure	3300		
		In the third year	
Organic manure	0	Cattle slurry	1200
Plant residues	1500	Plant residues	2400
(winter cereal)		(maize)	
Intercropping	500		
Mean annual carbon input to the soil	**5067**		**3600**

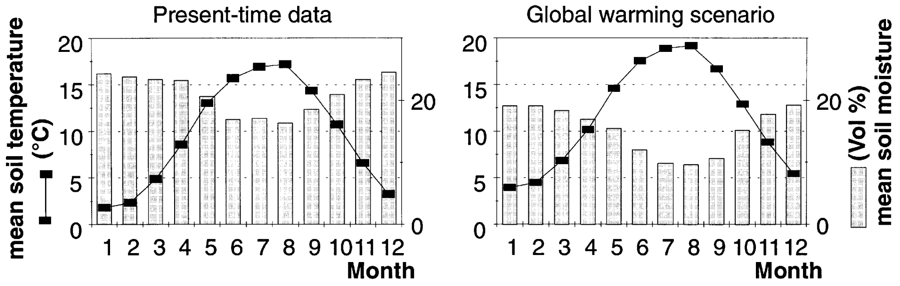

Figure 5. Monthly means of soil temperature and soil moisture under present-time conditions and in the “global warming scenario”.

not appear in these 30 year averages. The Q_{10}-value in the “global warming scenario” was lower throughout the year. The distance between the curves demonstrates a long-term trend due to global warming.

Figure 7 shows that the model calculations predict an increase of mean soil respiration during autumn, winter, and spring under global warming whereas

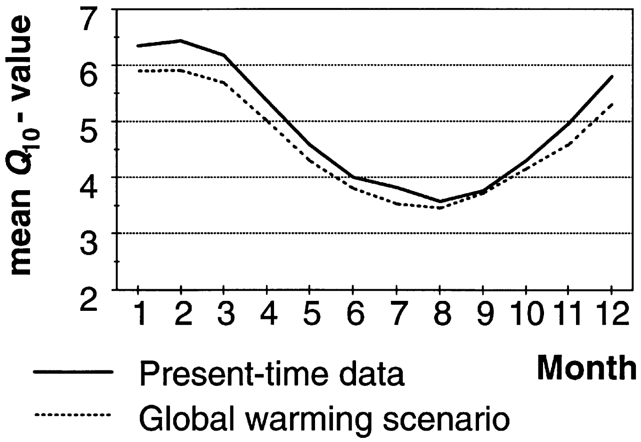

Figure 6. Monthly means of the Q_{10}-values under present-time conditions and in the "global warming scenario".

in the summer months with increased drought soil respiration is decreased. However, in the long run the mean annual soil respiration increases in both fields. During the whole period of thirty years with present climate conditions the SOC pool of the crop rotation field remains nearly constant due to the higher carbon inputs, whereas the maize monoculture field would lose about 16 t C ha^{-1}. These losses are the consequence of agricultural management with a permanent carbon deficit. In the global warming scenario the crop rotation field loses about 10 t C ha^{-1}, while more than 20 t C ha^{-1} are lost from the maize monoculture field.

The importance of the temperature and moisture adjustment of the Q_{10}-value can be shown by a comparison of the long-term effects of global warming and agricultural management (Figure 8). The global warming effects were set equal to the difference between the calculated soil organic carbon content after 30 years for the same field under different climate conditions. Both fields lost about 7 t carbon ha^{-1} due to the global warming effect. If a constant Q_{10}-value was assumed this effect was overestimated by the model by 16% for the crop rotation and underestimated by 12% for the maize monoculture. The effects of agricultural management were estimated by the difference between the resulting soil organic carbon content of the different treatments under the same climatic conditions (around 12 t ha^{-1} for both data sets). This difference was considerably overstimated by the model using a constant Q_{10}-value (34% under present climate conditions; 48% under global warming conditions).

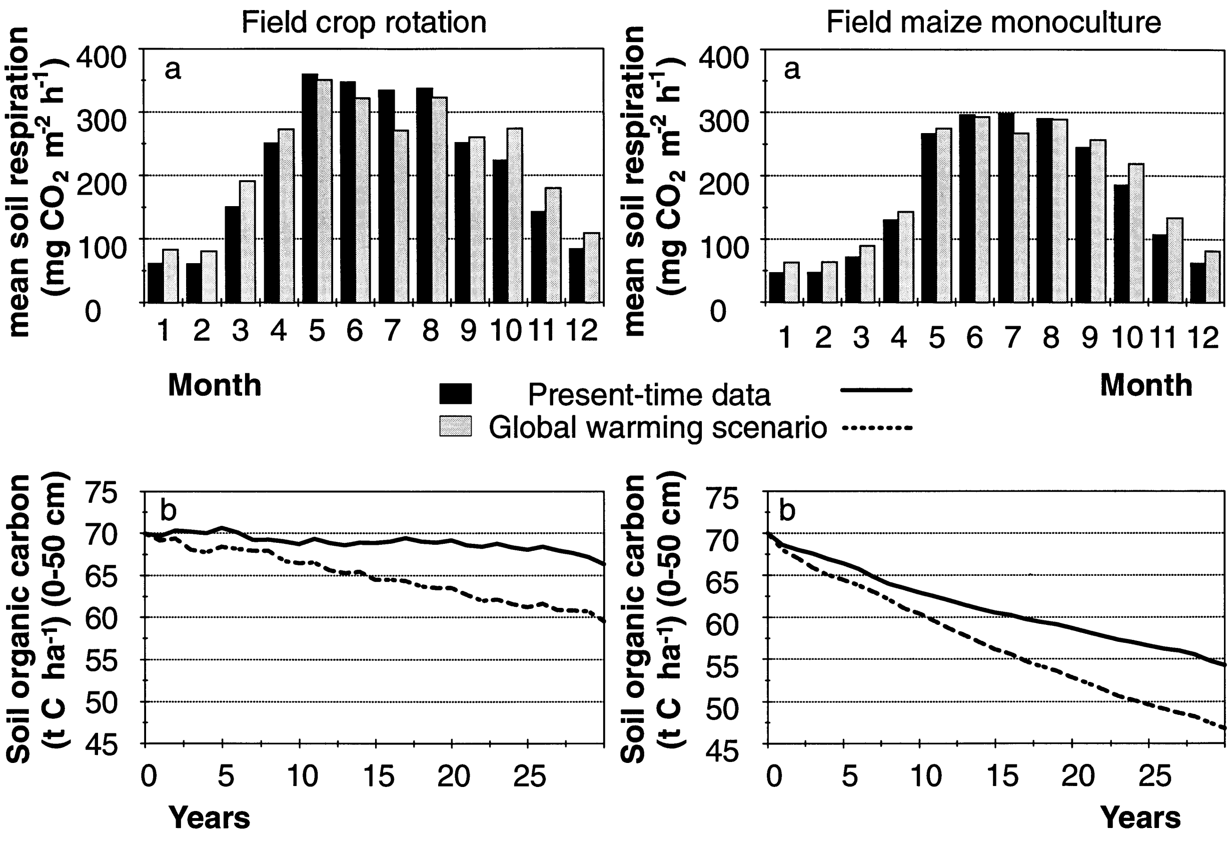

Figure 7. a: Monthly mean soil respiration (except root respiration) and b: long-term changes in soil organic carbon.

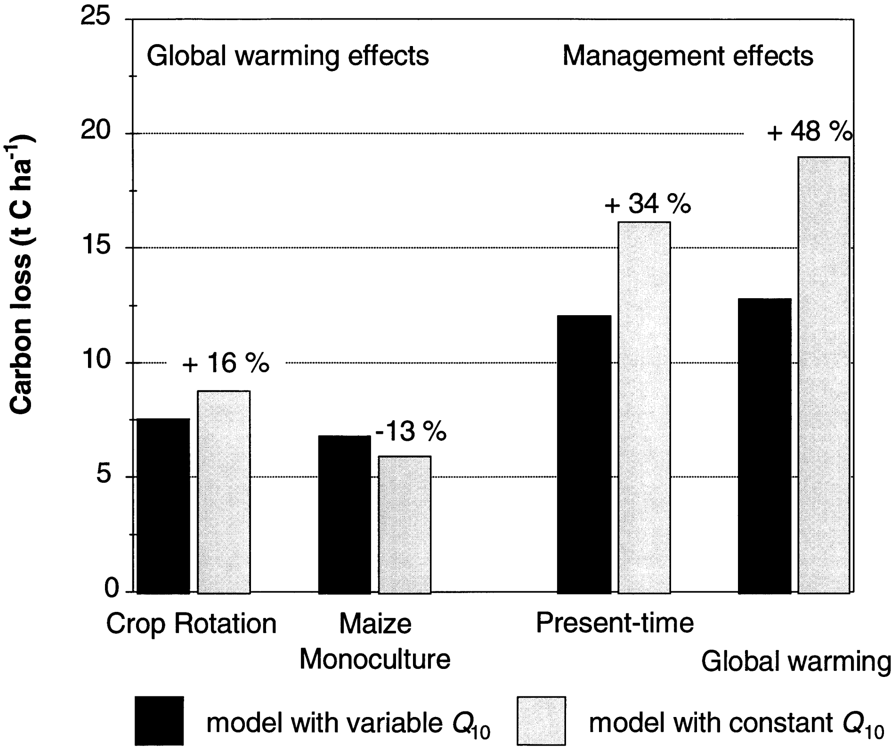

Figure 8. Long-term effects of global warming and agricultural managements on soil organic carbon. Black bars show the results of the model with variable Q_{10}. Grey bars show the results of the basic model with constant Q_{10}. The values above the grey bars indicate the difference between the model results (% of the model with variable Q_{10}).

Conclusions

By seasonal adjustment of the Q_{10}-value for soil respiration a soil biological system is able to buffer the impact of seasonal temperature variations. Like many other biological systems the edaphon tends to smoothen the impacts of temperature dynamics by adjustment. Though some explanations have been proposed for this phenomenon (Schneider & Kay 1994; Kappen et al., i.p.), our knowledge about the mechanisms underlying such an adjustment is scarce.

In the long-term simulations we could demonstrate a trend of decreasing Q_{10}-values as a consequence of global warming. This observation is in accordance with the data published by Kirschbaum (1995) for soil samples from warm and cold environments, which reflect long-term adjustments. Thus the consideration of a adjustable Q_{10}-value improves the quality of a mathematical soil respiration model. In long-term studies overestimation of carbon losses can be avoided.

Our case study indicates that increased soil respiration upon global warming causes a loss of soil organic carbon from soils in a temperate climate. The prediction is restricted to this scope because indirect effects of elevated CO_2 on soil respiration via NPP, substrate quality, and water use efficiency (O'Neill 1994; Cotrufo & Ineson 1995; Koch & Mooney 1996) were not taken into consideration. However, the agricultural management itself causes stronger impact on the soil organic carbon balance than the global warming effect. Dilly et al. (this issue) showed how landuse affected microbial biomass and activity. On a larger temporal and spatial scale monoculture plus addition of cattle slurry, without additional carbon supply, may be deleterious to agroecosystems by rapid depletion of soil organic carbon.

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References

Biscoe PV, Scott RK & Monteith JL (1975) Barley and its environment. III. Carbon budget of the stand. Journal of Applied Ecology 12: 269–291

Buyanovsky GA, Wagner GH & Gantzer CJ (1986) Soil respiration in a winter wheat ecosystem. Soil Sci. Soc. Am. Journal 50(2): 338–344

Carlyle JC & Than UB (1988) Abiotic controls of soil respiration beneath an eighteen-year-old *Pinus radiata* stand in south-eastern Australia. Journal of Ecology 76(3): 654–662

Cotrufo MF & Ineson P (1995) Effects of enhanced atmospheric CO_2 and nutrient supply on the quality and subsequent decomposition of fine roots of *Betula pendula* Roth. and *Picea sitchensis* (Bong.) Carr. Plant and Soil 170: 267–277

Cropper WP, Ewel KC & Raich JW (1985) The measurement of soil CO_2 evolution *in situ*. Pedobiologia 28: 35–40

Cubasch U, Hasselmann K, Höck H, Maier-Reimer E, Mikolajewicz U, Santer B & Sausen R (1992) Time-dependent greenhouse warming computations with a coupled ocean-atmosphere model. Climate Dynamics 8: 55–69

Dilly O, Mogge B, Kutsch WL, Kappen L & Munch JC (this issue) Aspects of carbon and nitrogen cycling in soils of the Bornhöved Lake Distict. I. Microbial characteristics and emissions of carbon dioxide and nitrous oxide of arable and grassland soils. Biogeochemistry (in press)

Edwards NT & Sollins P (1973) Continuous measurements of carbon dioxide evolution from partitioned forest floor components. Ecology 54: 406–412

Haber W (1958) Ökologische Untersuchung der Bodenatmung. Flora 146: 109–156

Hall AJ, Connor DJ & Whitfield DM (1990) Root respiration during grain filling in sunflower: The effects of water stress. Plant and Soil 121: 57–66

Hansen S, Jensen HE, Nielsen NE & Svendsen H (1990) DAISY – Soil Plant Atmosphere System Model. Miljöministeriet Miljöstyrelsen, Kopenhagen

Hoffmann F (1993) Die Ceres-Modelle – Übersicht, Weiterentwicklungen, Erfahrungen. In: Reiner L, Geidel H & Mangstl A (Eds) Agrarinformatik 24 (pp 139–150)

Hollwurtel E & Beinhauer R (1995) Klimaszenarien. EcoSys 2: 17–26, Kiel

Humfeld H (1930) A method for measuring carbon dioxide evolution from soil. Soil Science 30: 1–9

Jenkinson DS, Adams DE & Wild A (1991) Model estimates of CO_2 emissions from soil in response to global warming. Nature 351: 304–306

Kappen L, Kutsch WL, Müller F & Eschenbach C (in press) Hierarchical process interactions in the terrestrial carbon cycle – a comparison between forest and crop field. In: Beese & Hantschel (Eds) Processes in Managed Ecosystems: Spatial and Temporal Variability. Ecological Studies, Springer, Berlin, Heidelberg, New York

Kirschbaum MUF (1995) The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. Soil Biol. Biochem. 27: 753–760

Koch GW & Mooney HA (Eds) (1996) Carbon Dioxide and Terrestrial Ecosystems. Academic Press, Oxford

Koepf H (1953) Die Verwendung des URAS für die kontinuierliche Registrierung der Bodenatmung im Freiland. Landwirtschaftliche Forschung 5: 54–62

Koepf H (1954) Untersuchungen über die biologische Aktivität des Bodens. Teil I: Atmungskurven des Bodens und Fermentaktivität des Bodens. Z. f. Acker- und Pflanzenbau 98(3): 289–312

Kreyszik E (1982) Statistische Methoden und ihre Anwendungen, Vandenhoeck & Ruprecht, Göttingen

Krzysch G (1964) Zur Beeinflussung der Bodenatmung durch langjährige Düngungs- und Bodenbearbeitungsmaßnahmen. Z. f. Acker- und Pflanzenbau 120: 339–368

Kutsch W (1996) Untersuchungen zur Bodenatmung zweier Ackerstandorte im Bereich der Bornhöveder Seenkette. EcoSys, Kiel, Suppl. 16

Monteith JL, Szeicz G & Yabuki K (1964) Crop photosynthesis and the flux of carbon dioxide below the canopy. Journal of Applied Ecology 1: 321–337

O'Neill EG (1994) Responses of soil biota to elevated atmospheric carbon dioxide. Plant and Soil 165: 55–65

Orchard VA & Cook FJ (1983) Relationship between soil respiration and soil moisture. Soil Biol. Biochem. 15(4): 447–453

Porka, OH (1931) Über eine neue Methode zur Bestimmung der Bodenatmung. Ann. Soc. Zool. Bot. Fenn. 15: 101–108

Rochette P, Desjardins RL & Pattey E (1991) Spatial and temporal variability of soil respiration in agricultural fields. Can. J. Soil. Sci. 71: 189–196

Schneider ED & Kay JJ (1994) Life as a manifestation of the second law of thermodynamics. Mathl. Comput. Modelling 19: 25–48

Tardieu F (1988) Analysis of the spatial variability of maize root density. Plant and Soil 107: 259–266

Wynn-Williams DD (1982) Simulation of seasonal changes in microbial activity of maritime antarctic peat. Soil Biol. Biochem. 14(1): 1–12