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The effect of soil water content, soil temperature, soil pH-value and the root mass on soil CO_2 efflux – A modified model

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Abstract

To quantify the effects of soil temperature (T_{soil}), and relative soil water content (RSWC) on soil respiration we measured CO_2 soil efflux with a closed dynamic chamber *in situ* in the field and from soil cores in a controlled climate chamber experiment. Additionally we analysed the effect of soil acidity and fine root mass in the field. The analysis was performed on three meadow, two bare fallow and one forest sites. The influence of soil temperature on CO_2 emissions was highly significant with all land-use types, except for one field campaign with continuous rain. Where soil temperature had a significant influence, the percentage of variance explained by soil temperature varied from site to site from 13–46% in the field and 35–66% in the climate chamber. Changes of soil moisture influenced only the CO_2 efflux on meadow soils in field and climate chamber (14–34% explained variance), whereas on the bare soil and the forest soil there was no visible effect. The spatial variation of soil CO_2 emission in the field correlated significantly with the soil pH and fine root mass, explaining up to 24% and 31% of the variability. A non-linear regression model was developed to describe soil CO_2 efflux as a function of soil temperature, soil moisture, pH-value and root mass. With the model we could explain 60% of the variability in soil CO_2 emission of all individual field chamber measurements. Through the model analysis we highlight the temporal influence of rain events. The model overestimated the observed fluxes during and within four hours of the last rain event. Conversely, after more than 72 h without rain the model underestimated the fluxes. Between four and 72 h after rainfall, the regression model of soil CO_2 emission explained up to 91% of the variance.

Introduction

Soil CO_2 fluxes are the second major component of the global carbon cycle (Reich and Schlesinger 1992), and play an important role in climate change. Very often is it hypothesized that soils provide a positive feedback to climate warming due to the exponential response of soil CO_2 efflux to temperature (e.g. Cox et al., 2000; Kirschbaum, 1995). However, the gas exchange between the soil and the atmosphere depends on numerous complex and non-linear relationships, like physiological, biochemical, chemical, ecological and meteorological conditions (Jarvis, 1995; Schimel et al., 1994). Soil respiration represents the biological activity of the entire soil biota, including soil microbes (e.g. bacteria, fungi, algae, protozoa), plant roots and macroorganisms (e.g. earthworms, nematodes, insects). The rates of soil CO_2 efflux vary by ecosystem (Reich and Schlesinger, 1992) and are the major component of whole-ecosystem respiration, that in turn explains much of the continental gradient of the net carbon balance (Schulze et al., 1999; Valentini et al., 2000). So show Kelliher et al. (1999) and Law et al. (1999b) for forested ecosystems, that soil respiration amounts to 76–77% of the annual GPP, whereas agricultural crops during fallow periods act as a carbon emitter (Soegaard, 1999; Soegaard, et al. 2003). Despite these general trends emissions of CO_2 are highly spatially variable within one site (Law et al., 2001; Longdoz et al., 2000; Simek et al., 2004).

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A positive correlation between soil temperature and soil CO_2 efflux is well described by several reviews (Kätterer et al., 1998; Lloyd and Taylor, 1994; Reich and Schlesinger, 1992; Singh and Gupta, 1977). Also, soil moisture affects the soil CO_2 efflux (Bunnell et al., 1977; Orchard and Cook, 1983; Reichstein et al., 2002; Simek et al., 2004; Subke et al., 2003). Furthermore, soil CO_2 efflux is influenced by other factors like, substrate amount (Zak et al., 2000), the pH-value of the soil (Hall et al., 1997) as well as the activity of the vegetation (Reichstein et al., 2003b) since root respiration (Janssens et al., 1998; Kutsch et al., 2001; Law et al., 1999a) and heterotrophic respiration (Goulden et al., 1996; Hollinger et al., 1998) comprise total soil CO_2 efflux, and plants continuously excrete exudates into the soil. Several studies showed significant effects of soil pH values on soil respiration (Andersson and Nilsson, 2001; Hall et al., 1997; Sitaula et al., 1995) since, in particular, microbial activity increases with rising pH values (Ellis et al., 1998).

Furtheron, temporal effects like litter fall, decomposition dynamics and the amount and the timing of rainfall (Ball et al., 1999; Jackson et al., 1998) influence soil respiration. The effect of rainfall was often larger than expected from the relationship between soil moisture and CO_2 efflux (Davidson et al., 1998; Russell and Voroney, 1998).

A series of models try to explain the relationship between the factors governing soil CO_2 efflux. Most studies use different principles to describe temperature effects, e.g. linear regression analysis (Witkamp, 1966), Q_{10} (Maljanen et al., 2002; Reich and Schlesinger, 1992) or power relationship (Kucera and Kirkham, 1971), as well as relationships based on the Arrhenius form (Howard and Howard, 1979). However, all existing models cannot explain the total variation of the CO_2 soil efflux. Numerous empirical models were developed for crop (Boegh et al., 1999) and meadow soils (Bremer and Ham, 2002) or bare soils (Gupta et al., 1981; Reth et al., 2004). These models are not useful for forest soils. In contrast forest models (Baldocchi and Wilson, 2001; Janssens et al., 2001; Nakano et al., 2004; Rasse et al., 2001) are often of low use at bare soil or meadows.

The aim of this study is to analyse the influence of soil temperature, moisture, pH value and root mass on soil CO_2 efflux through a combination of field and laboratory experiments. In a second step these effects are assembled into an empirical model that should work on meadow and cropland as well as in forest and bare fallow soil. Finally, we explore a robust regression method to identify temporal effects on soil CO_2 efflux in the field that are not represented by the model.

Methods

Site description

The measurements used in this study were carried out in the course of special observation periods of the VERTIKO (Vertical transport under complex natural conditions) project, which is part of the AFO 2000 (German Atmospheric Research, 2000) programme. The target area of the VERTIKO project comprises the region between the Erzgebirge in the South and the Oder-Spree lake district in the North (100 km WE and 300 km NS). It includes a variety of natural small-scale variability from land use to orographic effects typical for Germany. During three special observation periods (SOPs) measurements were performed at anchor stations located in the target area. For an overview of the parameters observed during the field campaigns that are expected to influence soil CO_2 efflux see Table 1.

The measurements of SOP 1 were carried out in September and October 2001 at the Anchor Station Melpitz of the Institute for Tropospheric Research, located near Melpitz, Saxony (51°31′ N, 12°55′ E, 86 m a.s.l.). The area is a flat managed meadow (MW) of approximately 20 ha surrounded by farmland (MA, see e.g. Spindler et al., 2001). The annual mean air temperature is 8.7 °C and the annual precipitation 539 mm. The dominant species were *Lolium perenne, Taraxacum officinale* and *Leontodon autumnalis*. The leaf area index (LAI) was 2.0 $m^2\ m^{-2}$.

The SOP 2 experiment took place in June and July 2002 at the Falkenberg Boundary-Layer measurement site of the German Meteorological Service, the Lindenberg observatory, Brandenburg (52°10′ N, 14°07′ E, 73 m a.s.l.). The landscape in this region was formed by inland glaciers of the last ice age, with a slightly undulating orography and a heterogeneous land use structure (see e.g. Beyrich et al., 2002). The Falkenberg site itself is flat and consists of about 18 ha of managed meadow (LW) with short grass. An area of approximately 3 ha of the meadow was ploughed during the experiment (LA). The annual mean air temperature is 8.6 °C and the annual precipitation 560 mm. Main species were *Lolium perenne, Bromus hordeaceus, Festuca rubra, Leontodon autumnalis, Taraxacum officinale, Trifolium pratense* and

Table 1. Observed range of the parameters T_{soil} (soil temperature), RSWC (relative soil water content), pH and RRM (fine root biomass, d.w. based) expected to influence soil CO_2 emission during the field campaigns (MW = Melpitz Meadow, MA = Melpitz Agricultural Fallow, LW = Lindenberg Meadow, LA = Lindenberg Agricultural Fallow, TW = Tharandt Meadow, TF = Tharandt Forest)

	T_{soil} min (°C)	T_{soil} max (°C)	RSWC min (%)	RSWC max (%)	pH min	pH max	RRm min (%)	RRM max (%)
MW	10.3	16.6	3	98	5.8	7.1	0.035	9
MA	10.7	21.5	39	99	6.9	7.4	0	0
LW	14.3	25.8	17	38	4.5	6.9	0.41	26
LA	14.5	18.9	16	17	5.0	5.9	0	0
TW	11.5	20.9	58	97	5.0	5.5	2	6
TF	9.0	18.6	56	81	3.3	3.8	0.36	36

Trifolium repens. Meadow LAI showed a spatial gradient during the field campaign, with maximum LAI of 4.7, and minimum LAI of 1.3 m^2 m^{-2}.

The SOP 3 measurements were performed in May and June 2003 at the Anchor Station Tharandter Wald of the Technical University Dresden near Tharandt, Saxony (50°58′ N, 13°34′ E, 375 m a.s.l.). The slightly undulating experimental area is located inside a closed forest of approximately 6000 ha. The annual mean air temperature is 7.6 °C and the annual precipitation 820 mm. The forest (TF) is dominated by 114 years old, approximately 28 m high *Picea abies* (L.) KARST trees. The projected leaf area index (LAI) was 6.9 m^2 m^{-2}. The meadow area (TW) of the anchor station is 1.5 ha and dominated by *Rumex obtusifolium* (L.), *Holcus lanatus* (L.), *Cirsium arvense* (L.) and *Carex* spp. The leaf area of the meadow was 2.6 m^2 m^{-2} at the beginning (May, 22) of the flux measurements and increased to 6.1 m^2 m^{-2} at the end of the campaign (June, 13).

These field measurements were complemented by climate chamber experiments to extend the range of soil temperatures and soil moisture observed during the SOPs.

Soil efflux and soil analysis in the field

Soil CO_2 efflux was measured with a non-steady-state flow-through chamber system, and fluxes were determined from the concentration increase in closed chambers. The system consists of cylindrical steel chambers (height 80 mm and diameter 197 mm) with plexi glass lids attached during the measurement. No fan was used in the system. Overheating could be avoided because single measurements were completed within 12 min, and soil temperatures inside and outside the chamber differed less than 0.2 °C. The chambers were inserted 2 cm into the soil and all plant material was removed from the chambers' interiors. The first flux measurements started approximately 12 h after plant cutting to avoid effects on soil CO_2 efflux by collar insertion or plant cutting. Collars remained in place during all subsequent measurements at the site. Ten chambers were installed as spatial replicates at each land use type, except at the bare soil of Lindenberg with only five chambers. Measurements took place from the early morning to late in the evening. The chambers were moved to another site or land use after finishing 5 to 14 measurements at the same point. The system allowed to measure five chambers alternately with magnetic valves controlling the flow of the different chambers. For the concentration measurements the air was pumped in a closed loop from the chamber to the analyser (Photoacoustic Multi-gas Monitor, INNOVA 1312) and back to the chamber. Through a 20 m long tube with an inside diameter of 3 mm, the air was sucked for approximately 30 s with a speed of 4 m s^{-1}. The concentrations of CO_2 (for control) and water were determined from the air stream. The CO_2 efflux was determined from the slope of the concentration increase within a chamber using four concentrations measured at 238 s intervals. The system was tested against other measurement systems (non-steady-state flow-through chambers, non-steady-state non-flow-through chambers, non-steady-state non-flow-through chambers and a calibration system) in a calibration experiment (Pumpanen et al., 2004). In this experiment he system employed showed an underestimation of approximately 4% for soils comparable to those in this study, and at maximum 11% for dry fine sand.

Parallel to the soil flux measurements environmental parameters were observed quasi-continuously. Soil temperature (Thermistor, Siemens M841) was recorded at 2 cm depth inside each chamber and outside the chambers every 5 min. Volumetric soil water content (SWC, m^3 water per m^3 total soil volume, Theta Probe, ML2) was measured half hourly in the upper 10 cm of the soil at each stand. Relative soil water content (RSWC) is defined as SWC divided by field capacity, allowing for a better comparison of soils with different textures. Reichstein et al. (2002) found very similar $RSWC_{1/2}$ parameters for a sandy and clayey soil, Nevertheless one would not expect exactly the same values of $RSWC_{1/2}$ in all soils, and our assumption that reduces the number of model parameters introduces (albeit little) model error.

Analysis of root mass and pH of soil samples of each chamber were performed after finishing flux measurements. Soil cores with a diameter of 5 cm and a depth of 10 cm were taken in the field, and soil and roots were separated manually. The remaining soil was sieved to remove stones. The root biomass was dried three days at 105 °C. The dry mass of the roots was expressed per unit dry mass of the oven-dry soil. The pH-value was determined from a fresh soil slurry using a glass electrode (Scheffer and Schachtschabel, 2002). Incubation time of 20 g soil was 1 h in 50 g distilled water.

Soil efflux in the climate chamber

For the climate chamber experiments five replicate fresh soil cores (diameter = 31 cm, height = 25 cm) were collected under minimal disturbance from the meadow of Melpitz, Lindenberg and Tharandt as well as from the fallow of Lindenberg and the forest of Tharandt. CO_2 efflux of the soil samples was recorded over 112 days. Soil temperature was manipulated by changing the air temperature inside the climate chamber. Starting at 20 °C the soil temperature was decreased every two days by 2 °C. After reaching 4 °C the soil temperature was increased every two days by 2 oC up to 38 °C, then decreased again and so forth. Soil water content was altered by irrigation and drying cycles. At beginning and end of each flux measurement (for description of the system see above), we weighed the soil cores for gravimetric determination of soil water content. In the climate chamber it was not possible to analyse the soil without destroying the soil cores. Therefore the soils were not analysed for the parameters pH and RRM.

Soil CO_2 model

The non-linear regression model of soil CO_2 efflux was adapted from Reichstein et al. (2003b, 2002) that includes a function for soil temperature (T_{soil}, Equation 3) – following an exponential response, a function of relative soil water content (RSWC, Equation 4) and a function of vegetation activity. We modified the model by Reichstein (2003b) for better incorporation of the actually measured data in two ways: (1) The soil CO_2 emission rate under standard conditions, was made dependent on root mass per soil mass as a proxy for vegetation activity (instead of leaf area index in Reichstein, et al. 2003b); (2) We included the influence of soil chemistry through including the soil pH as additional predictor. Mathematically, the model is described by the following equations:

$$R_{soil} = R_{ref} * F(T_{soil}) * g(RSWC) * h(pH), \qquad (1)$$

where R_{soil} is the soil CO_2 efflux. The emission under standard conditions (R_{ref}), at T_{ref} and non-limiting soil water content, is described by:

$$R_{ref} = H_{resp} + a_{resp}, \qquad (2)$$

where h_{resp} represents heterotrophic respiration and a_{resp} autotrophic respiration. The heterotrophic respiration is a fitted parameter and a_{resp} is a linear function of the root mass per dry soil mass (RRM) and a parameter (rf):

$$a_{resp} = RRM * rf. \qquad (3)$$

The exponential increase of the CO_2 emission with soil temperature is described by:

$$\mathrm{f}(T_{soil}) = \exp\left(E_0 * \left(\frac{1}{T_{ref} - T_0} - \frac{1}{T_{soil} - T_0}\right)\right), \qquad (4)$$

where E_0 is a free parameter analogue to the activation energy in the standard Arrhenius model, T_{ref} is the reference soil temperature and T_0 the lower temperature limit for R_{soil}. T_{ref} was set to 15 °C and T_0 at −46.02 °C (Lloyd and Taylor, 1994). The response of changes on relative soil water content is described by:

$$\mathrm{g}(RSWC) = \frac{RSWC - RSWC_0}{(RSWC_{1/2} - RSWC_0) + (RSWC - RSWC_0)}. \qquad (5)$$

$RSWC_{1/2}$ represents the RSWC at half-maximum soil CO_2 efflux and RSWC0 is the residual soil water content, below which the efflux ceases. $RSWC_{1/2}$ and $RSWC_0$ are free parameters. Finally, the response of the CO_2 emission with soil pH-value follows an optimum curve:

Table 2. Coefficients of variation for the univariate analysis of soil CO_2 emission influencing parameters during the field (FM) and the climate chamber measurements (CCM). T_{soil} (soil temperature), RSWC (relative soil water content), pH and RRM (fine root biomass, d.w. based), n represents the number of CO_2 flux observations not affected by rain, and used for the regression model parameterisation. For site abbreviations see Table 1

	FM					CCM	
	T_{soil}	RSWC	RRM	pH	n	T_{soil}	RSWC
MW	0^{+}	0^{+}	0^{+}	0^{+}	0	0.45*	0.1
MA	0^{+}	0^{+}	ND	0^{+}	0	0.35*	0.09
LW	0.25*	0.34*	0.12*	0.19*	141	0.52*	0
LA	0.46*	0	ND	0.24*	30	ND	ND
TW	0.31*	0.18*	0.3*	0.19*	50	0.65*	0.14*
TF	0.13*	0.04	0.31*	0.23*	74	0.66*	0

$^{*}P < 0.01$, ND = not determined.
$^{+}$not used for model parameterisation.

$$\mathrm{h}(pH) = \exp\left(-\left(\frac{pH - phOpt}{phSens}\right)^2\right), \qquad (6)$$

where phOpt is a free parameter and represents the optimal pH value. The parameter phSens describes the sensitivity of soil CO_2 efflux to deviation from this optimal value.

Parameter estimation

For the data analysis with the non-linear regression model we used a robust regression technique that is able to objectively identify outliers, or more precisely data points, that are inconsistent with the model assumptions. We used the non-linear least trimmed squares (LTS) regression (Reichstein et al., 2003a; Stromberg, 1997), that seeks to minimize the sum of squared residuals as ordinary non-linear regression, but with exclusion of the largest x % of residuals, that are assumed to be due to contaminated data or due to data inconsistent with the model. Formally the objective function that has to be minimised is the trimmed sum of squared errors (TSSE):

$$TSSE = \sum_{i \le N\cdot(1-0.001-t)} r_i^2, \qquad (7)$$

where r_i is the i-th smallest residual, N is the total number of data points, and (0.01t) is the fraction of residuals to be excluded. The procedure was performed with trimming percentages of 10, 20, 30% and subsequently analysed which data was classified as ‘contaminated’ by the procedure.

Results

We examined the effect of soil temperature changes on CO_2 efflux at the four soil types of the field measurements and of five soil types in the climate chamber experiment. Due to the continuous rain during SOP 1, the results of the field measurements in Melpitz were not used in the temperature, and all further analyses. An exponential increase with increasing soil temperature was observed at all soils (Figure 1), both during the field measurements and in the climate chamber experiment (Table 2).

Meadow soils, except MW in both field and climate chamber measurements, and LW in the climate chamber measurements, responded to changes of relative soil water content. There was no statistically significant effect at the fallow and the forest soil, both in the field and in the climate chamber measurements (Table 2).

Variation of the pH-value of the soils and between the single measurement points at each site showed a positive correlation with the CO_2 efflux (Figure 2). During simultaneous measurements with similar soil temperature and soil water content, the chambers with higher soil pH exhibited higher CO_2 fluxes, except in Melpitz (Table 2).

Also the presence of fine roots significantly affected the observed soil CO_2 efflux. At all meadow and forest stands, again except for Melpitz, the relative root mass was correlated positively (Figure 3) with the CO_2 flux rates (Table 2).

While the univariate relationships between soil CO_2 efflux and environmental factors were generally weak, the above soil CO_2 efflux model already

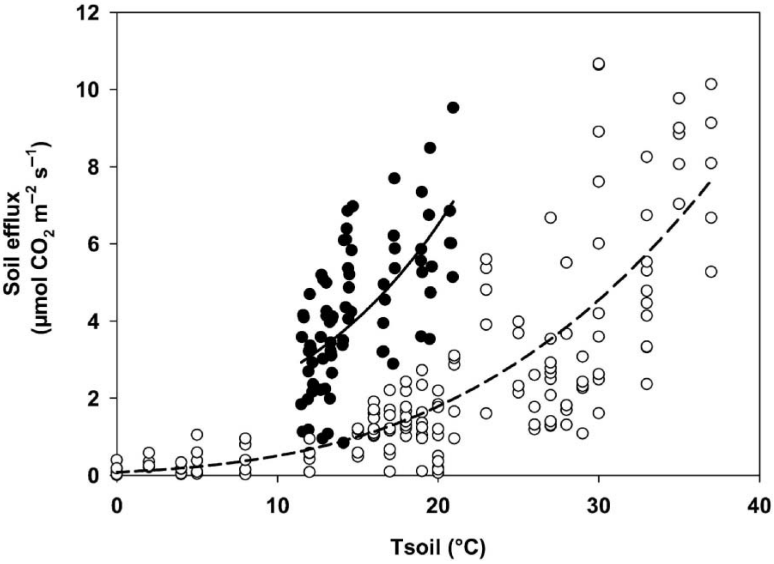

Figure 1. Soil CO_2 efflux as an exponential function of soil temperature (T_{soil}) for the meadow soil of Tharandt (TW) in the field (closed dots, $r^2 = 0.31$), and in the climate chamber (open dots, $r^2 = 0.65$). The lines are regression lines, calculated from the used data using equation 4.

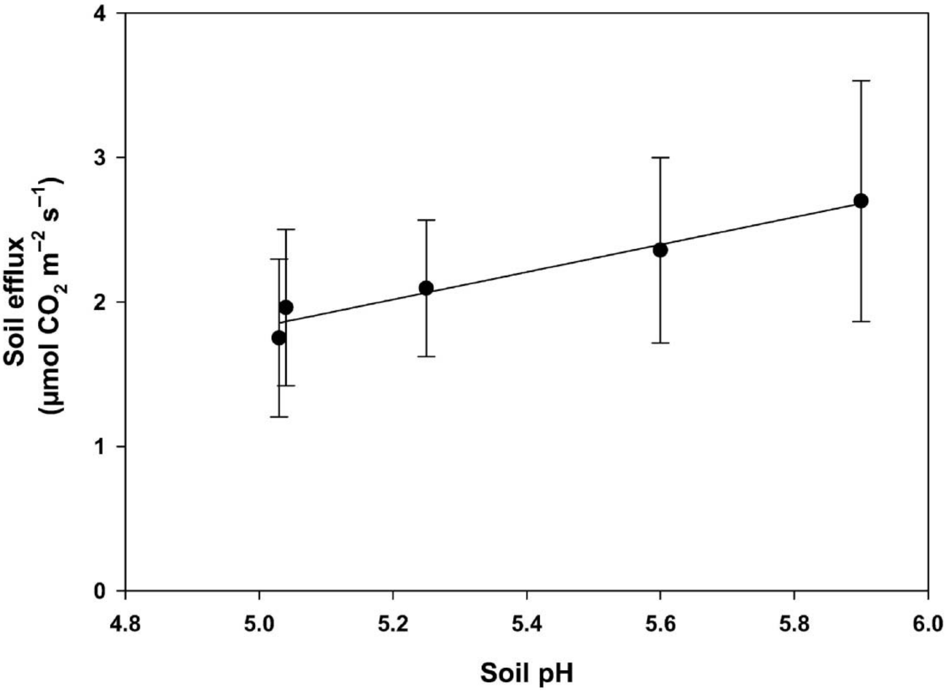

Figure 2. Soil CO_2 efflux as function of soil pH-value at the fallow in Lindenberg (LA). Dots represent the mean CO_2 fluxes ($n = 5$) with error bars ($r^2 = 0.24$). The line is the regression line, calculated from the used data using equation 6.

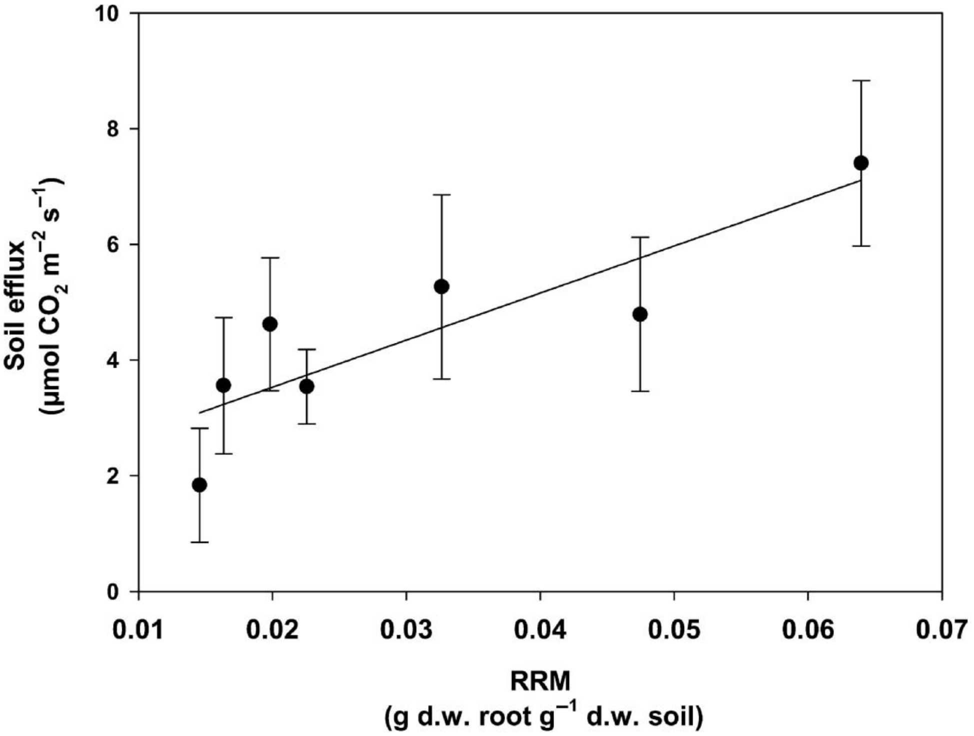

Figure 3. Soil CO_2 efflux as function of relative root mass (RMM) at the meadow soil of Tharandt (TW). Dots represent the mean CO_2 fluxes ($n = 6$) with standard deviation ($r^2 = 0.30$). The line is the regression line, calculated from the used data using equation 3.

explained 60% of the variability of soil CO_2 efflux (Figure 4a). With the robust regression approach we analysed inconsistence of the model (Figure 4b–d). 30% of the data could be identified as inconsistent with the model and could be related to disturbance by precipitation events (Figure 4e).

Thereby we could identify 3 periods: During and up to 4 h after a rain event (period 1) the model overestimated the measured CO_2 fluxes. In contrast, after a dry period of more than 72 h (period 2) the model underestimated the fluxes. In the time period in between, that is 4 to 72 h after the last rain event (period 3), the model reflected the measured emissions well, and explained 91% of their variability (Table 3). Interestingly, the amount of rain did not affect the performance of the model. The robust regression method rejected 87% of the data points falling into period 1 or 3, supporting the rationale to identify and exclude data that are inconsistent with the model.

Discussion

In this paper we confirmed well known correlations of soil CO_2 efflux and abiotic factors, although sometimes the ranges of driving forces in the field were too small to detect previously reported effects, e.g. on Q_{10}.

The strong correlation of temperature and soil CO_2 emission was quantified for many soils under different conditions (see e.g. Epron et al., 1999; Kätterer et al., 1998; Lloyd and Taylor, 1994; Reich and Schlesinger, 1992). In our climate chamber measurements, all soils showed an exponential increase of soil CO_2 efflux with increasing soil temperature ($P < 0.01$). In the field the soil CO_2 efflux was more variable, indicating increasing influence of other parameters.

A similar distinction was observed comparing soil CO_2 exchanges at changing soil moisture. Only at the meadow stands in Tharandt and in the field measurements of Lindenberg soil CO_2 efflux showed significant ($P < 0.01$) response to soil moisture changes. At the other stands, and partly during the climate chamber experiments, the relative soil water content span allowed only for small limiting effects due to soil water. Also, Reichstein et al. (2003b) observed a broad range

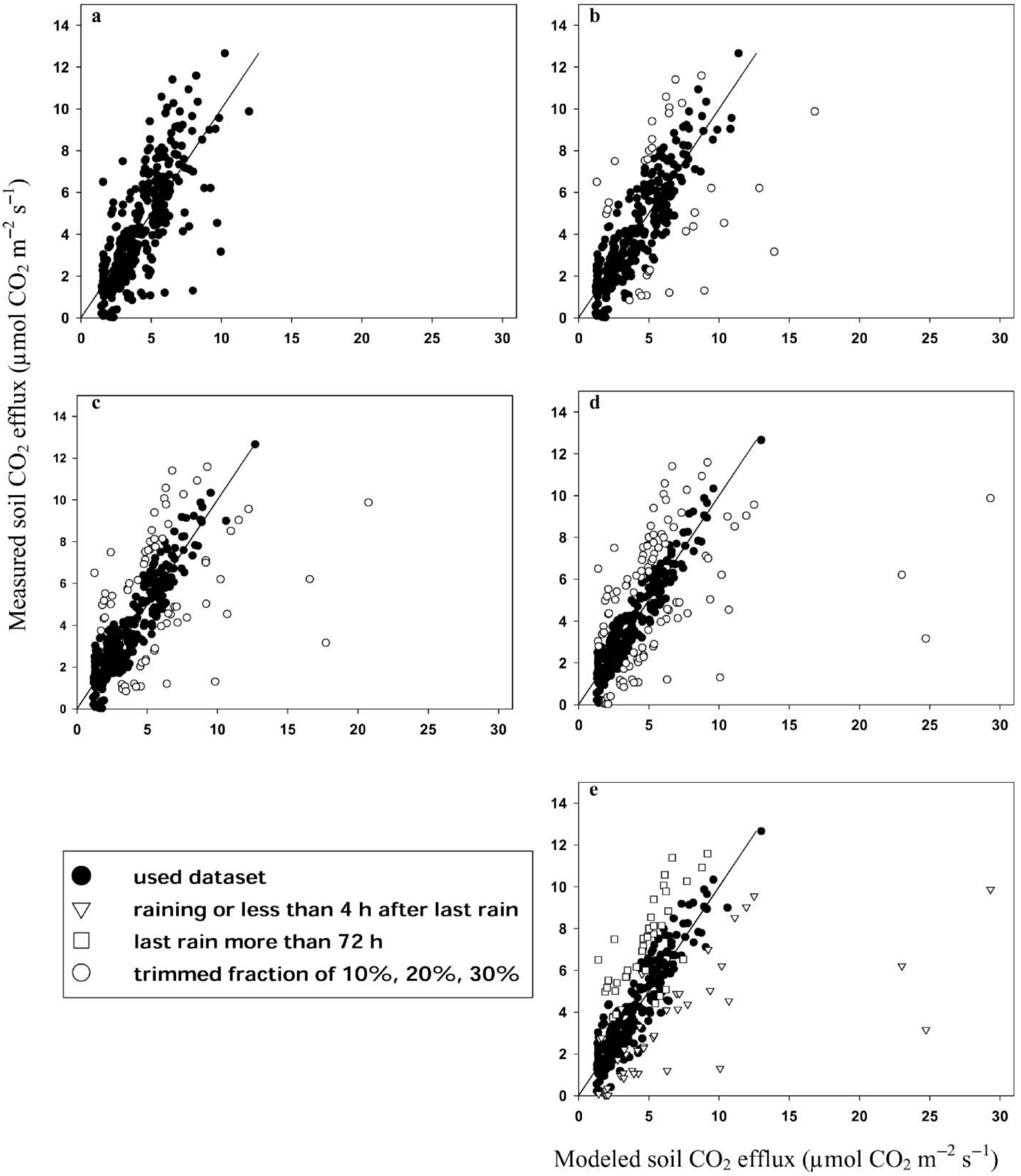

Figure 4. Comparison of modeled and measured soil CO_2 efflux: (a) without a trimmed fraction ($r^2 = 0.60$), (b) with a trimmed fraction of 10% ($r^2 = 0.80$), (c) with a trimmed fraction of 20% ($r^2 = 0.86$), (d) with a trimmed fraction of 30% ($r^2 = 0.91$) and (e) evaluating the temporal effect of last rain event. Lines are 1:1 lines.

Table 3. Parameters of the nonlinear regression model for all stands with a trimmed fraction of 30% ($n = 295$). 240 values were not effected by rain or drought, and indicated as consistent with the model (LW: $n = 97$, LA: $n = 30$, TW: $n = 44$, TF: $n = 69$). Root mean square error (RMSE) of the model results was 0.89 μmol m^{-2} s^{-1}. To take into account the 4% underestimation of the system (Pumpanen et al., 2004), the parameters h_{resp} and rf have to be multiplied with the correction factor 0.96

Parameter	Units	Value	Standard error
h_{resp}	μmol m^{-2} s^{-1}	9.11	2.12
E_0	K	247.78	16.84
$RSWC_0$	%	9	2
$RSWC_{1/2}$	%	17	0.9
phOpt		9.35	1.23
phSens		−4.87	0.69
rf	μmol m^{-2} s^{-1} g d.w.	19.91	5.23
Soil (g d.w. root)$^{-1}$			

of near optimum soil water content where changes in soil moisture have little or no effect and correspond to our observations. At the bare soil of SOP 2 at Lindenberg the soil water content was nearly constant while the measurements were performed, so there was no effect of soil moisture changes on CO_2 efflux at this time.

Even when taking soil temperature and water content into account, the spatial variation of soil CO_2 efflux at one site can be large. Buchmann (2000) reported spatial variations among soil collars, which were larger than the diurnal variability of soil CO_2 emission rates measured with the same collars during a day. This corresponds well with our field measurements, in particular at the forest stand, where soil temperature changes were very small, but spatial variability was high. Thus, multivariate interaction of various other factors has to be accounted for as in the model presented here.

The link of respiration to vegetation productivity established by Reichstein et al. (2003b) with potentially confounding factors at the continental scale, was here confirmed at small scale for soil CO_2 efflux. Anderson (1992) and Janssens et al. (1998) showed, that root respiration may account for half of the soil efflux. In general, this agreed with our observations for the forest and meadow sites. In addition, samples with higher root mass per soil showed higher CO_2 emission ($P < 0.01$) at comparable meteorological conditions. This finding held within a site, but not among different sites, where other factors determined the overall magnitude of soil CO_2 efflux.

An influence of spatial heterogeneity of soil pH on soil CO_2 emission was confirmed at all stands ($P < 0.01$), except Melpitz. Several studies described a similar positive correlation of pH-value and soil CO_2 efflux (Andersson and Nilsson, 2001; Ellis et al., 1998; Hall et al., 1997; Sitaula et al., 1995). Baath (1996) and Högberg et al. (2003) demonstrated the direct positive effect on soil respiration with pH tolerance of the bacterial community. A biological activity of soil microorganisms is permitted between a soil pH of a minimum of 3 and a maximum of 7 to 8 (Scheffer and Schachtschabel, 2002). Between these values (see Table 1), and otherwise constant conditions we observed a nearly linear increase of soil CO_2 emission. In the model however, we described the response to soil pH with an optimum curve to account for potential decline in soil CO_2 emission above a pH of 9. Similar pattern were shown in Wittmann et al. (2004) with an optimum curve for the dependence of hydrolytic enzyme activities in a forest soil.

The nonlinear regression model gave good results for all investigated sites. Up to 60% of the data variance could be explained by soil temperature, relative soil water content, soil pH and relative root mass. Evaluating the time span between measurement and last occurring rain, the modeled soil CO_2 effluxes overestimated the measured fluxes in the case of rain or maximum 4 h after the last rain. The main cause for this could be the reduction of the soil air-filled pore space resulting in reduced gaseous diffusivities. The negative effect of water filled pores on soil CO_2 emission is often discussed in the literature (see e.g. Ball et al., 1999; Lee et al., 2002).

After three or more days without rain, the model underestimated the observed fluxes. An explanation for this might be a shift of the main respiratory activity to deeper soil layers, with soil moisture and temperatures more favourable to respiration than those recorded by the sensors in the top soil layer. Another explanation could be that fine roots dying in the upper soil, and new root development in deeper soil layers led to an increase in CO_2 release. For the time between 4 and 72 h after a rain event, the model worked well, explaining 91% of the soil efflux variation with changes in soil temperature, soil water content, root mass and soil pH.

Potential limitation of the model could be that the temperature, soil water content, and pH responses of respiration arising from roots and soil heterotrophs might differ. Root respiration depends on current photosynthetic products as substrate, and is therefore mainly controlled by light availability during the last 2 days (Fitter et al., 1998). Heteorotrophs use older photosynthetic products (e.g. litter, turnover of fine roots), but also use root exudates (Grayston et al., 1997), as rhizosphere micro-organisms rapidly acquire the isotopic signature of the current photosynthate (Pendall et al., 2003), therefore being partly coupled to light availability too. In our case, we had to simplify these effects, as it was not possible to separate the responses of these two component fluxes from data measured with our technique. We included only the relative amounts of autotrophic and heterotrophic respiration in the model, and applied identical temperature, soil water content, and pH functions.

We tried to overcome the limiting effects of relatively short measurement campaigns at the various sites with soil cores taken to the climate chamber for wider ranges of temperature and moisture. However, this setup still did not allow for proper assessment of threshold events or sudden shifts in key variables determining soil respiration or soil CO_2 efflux. Yet in the field, Jensen et al. (1996), Lee et al. (2002) and Rey et al. (2002) observed a steep increase of CO_2 efflux with the first rain after drought, indicating dynamic effects on soil CO_2 efflux. However, with our method we could identify periods in our field data set that were not consistent with our static model by the robust regression approach. As we removed aboveground plant material before the measurements of soil CO_2 efflux, and determined only root biomass, we were not able to include the dynamic effects of root activity, or current photosynthates on root and heterotrophic respiration.

Due to these limitations our model might be restricted from its formulation and parameterisation to finer time scales, yet we believe that the model can be used for long-term predictions (up to a year), when coupled to a prognostic model for soil moisture, temperature, fine root biomass and pH. The model equations per se do not allow for feedbacks, dynamic responses or nonlinear (sensu strictu) events, but could enhance current generation carbon cycle models, which mainly concentrate on temperature effects (e.g. Cox et al., 2000), with additional factors as soil moisture, fine root biomass and pH, to help address complex ecological relationships to identify feedbacks between soil respiration and climate change.

We have shown that the robust regression approach is very useful as an objective means of ecological data analysis, when carefully interpreted. Through this approach we obtained parameters that are valid for normal conditions and that describe the data very well, while at the same time highlighting model problems under non-normal, transient conditions, namely during or shortly after rain events or after longer periods (>72 h) of dry conditions. With a standard regression approach on the contrary, one would have got average, effective parameters that are affected by the conditions under which the model is not valid, and thus are 'fitted' parameters in the bad sense of the word. The robust regression approach helps to avoid including periods in the parameterisation that are beyond the scope of the model, e.g. transient changes in diffusion pathways or location and status of biological activity and lead to unwanted errors even in the range where the model could be valid. Moreover, we determined 4 to 72 h as the time scale for our investigated systems, where a model based on steady-state conditions is suitable when accounting for changes in soil temperature, moisture, pH and fine root biomass.

Conclusion

In this study we developed a model that allows estimation of soil CO_2 efflux on bare soils, meadow soils as well as forest soils. The study confirmed soil temperature and soil water content as the most important factors influencing soil CO_2 emission. In addition soil pH and relative root mass are found as important factors to describe spatial variation of soil CO_2 emission due to vegetation productivity and microbial activity spans.

We explored the potential of the robust regression approach for determining valid parameter estimates and identifying the application scope of the model. From our experience, we advocate the exploration of this method in other ecological studies.

With respect to temporal and spatial dynamics in fine root and microbial activity, and soil physical properties (water filled pore space), there is a need to extend the model with either temporal varying parameters or dynamic model formulation.

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