Explaining temporal variation in soil CO$_2$ efflux in a mature spruce forest in Southern Germany

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Abstract

An open dynamic chamber system was used to measure the soil CO$_2$ efflux intensively and continuously throughout a growing season in a mature spruce forest (Picea abies) in Southern Germany. The resulting data set contained a large amount of temporally highly resolved information on the variation in soil CO$_2$ efflux together with environmental variables. Based on this background, the dependencies of the soil CO$_2$ efflux rate on the controlling environmental factors were analysed in-depth. Of the abiotic factors, soil temperature alone explained 72% of the variation in the efflux rate, and including soil water content (SWC) as an additional variable increased the explained variance to about 83%. Between April and December, average rates ranged from 0.43 to 5.15 µmol CO$_2$ m$^{-2}$ s$^{-1}$ (in November and July, respectively) with diurnal variations of up to 50% throughout the experiment. The variability in wind speed above the forest floor influenced the CO$_2$ efflux rates for measuring locations with a litter layer of relatively low bulk density (and hence relatively high proportions of pore spaces). For the temporal integration of flux rates for time scales of hours to days, however, wind velocities were of no effect, reflecting the fact that wind forcing acts on the transport, but not the production of CO$_2$ in the soil. The variation in both the magnitude of the basal respiration rate and the temperature sensitivity throughout the growing season was only moderate (coefficient of variation of 15 and 25%, respectively). Soil water limitation of the CO$_2$ production in the soil could be best explained by a reduction in the temperature-insensitive basal respiration rate, with no discernible effect on the temperature sensitivity. Using a soil CO$_2$ efflux model with soil temperature and SWC as driving variables, it was possible to calculate the annual soil CO$_2$ efflux for four consecutive years for which meteorological data were available. These simulations indicate an average efflux sum of 560 g C m$^{-2}$ yr$^{-1}$ (SE = 22 g C m$^{-2}$ yr$^{-1}$). An alternative model derived from the same data but using temperature alone as a driver over-estimated the annual flux sum by about 7% and showed less inter-annual variability. Given a likely shift in precipitation patterns alongside temperature changes under projected global change scenarios, these results demonstrate the necessity to include soil moisture in models that calculate the evolution of CO$_2$ from temperate forest soils.

Keywords: Carbon cycle; Open dynamic chamber; Picea abies; CO$_2$ efflux; Soil temperature; Soil water content

1. Introduction

Recent publications indicate that the terrestrial biosphere is acting as a C sink (Valentini et al., 2000; Schimel et al., 2001; IPCC, 2001), thus mitigating a potential global warming due to radiative forcing by anthropogenic emissions of so-called greenhouse gases (mostly CO$_2$ and CH$_4$, but also N$_2$O and halocarbons). Most of the C bound in the terrestrial biosphere is found in the soil (IPCC, 2000), with a general trend of increasing C storage with decreasing annual average temperatures (Parton et al., 1987; Houghton, 1995). It is the reaction of this largest of all pools to changes in climate, which will determine whether ecosystems will continue to absorb CO$_2$ from the atmosphere, or whether increased decomposition of soil organic matter (SOM) will eventually turn present C sinks into C sources.

The decomposition of SOM is a function of environmental variables (both physical and chemical) and the composition of the SOM. The changes in chemical composition of organic material with age affect the rate at which certain fractions of the total SOM pool can be decomposed (Berg et al., 1996; Coutteaux et al., 1998; Berg, 2000). While most of freshly added organic material decomposes readily after a few years (Bohn et al., 1985), the remainder becomes part of a more inert, or stable C pool...
within the soil. In the absence of disturbance, SOM accumulation can continue over centuries or even millennia (Jenny, 1980; Bohn et al., 1985; Liski, 1997). The temperature sensitivity of this old fraction of SOM is critical, since a global trend towards higher annual mean temperatures would create a positive feedback for global change. If this persistent fraction of SOM is tolerant of rising temperatures, as is indicated by some results (Liski et al., 1999), the present C sink may prevail or even strengthen (Grace and Rayment, 2000; Thornley and Cannell, 2001). However, this temperature insensitivity of old SOM has been disputed by Ågren (1999), who cites other results indicating that old SOM is indeed sensitive to temperature. Trumbore (2000), however, cautions that extrapolations of research findings (on which the models mentioned here are founded) have to account for the heterogeneity of the C stock since storage calculations will otherwise under-estimate short-term storage and over-estimate long-term storage of C. Changes in the allocation of assimilated C to roots and root turnover following climatic change may provide yet another process that affects C storage below ground (Norby and Jackson, 2000) which is only poorly understood, and hence not reflected in ecosystem models.

The picture emerging from these ongoing trends in ecosystem research shows that reliable predictions about the behaviour of ecosystems with respect to their C storage potential are only possible if the below-ground processes are better understood. There is a considerable amount of literature covering the efflux dependencies of CO₂ from forest soils, covering a wide range of sampling strategies. However, most studies are based on sporadic sampling of the soil CO₂ efflux, or misrepresent seasonal effects by too short sampling campaigns. We have made an in-depth analysis of the factors influencing the CO₂ efflux from soil based on data collected throughout an entire growing season in a mature spruce forest located in a small mountain range in Southern Germany.

2. Methods

2.1. Site description

The ‘Weidenbrunnen 2’ site is a 112-yr-old Norway spruce stand (Picea abies (L.) Karst.) at about 760 m elevation in the Fichtelgebirge, a mountain range in northern Bavaria (SE Germany; 50°08’N, 11°52’E). The local soil type was classified as cambic podzol over granitic bedrock characterised by low pH values (3.3–3.9; Heindl and Bott, 1995). Soil litter and the organic horizon had an average thickness of 1.6 and 15 cm, respectively, with roughly equal thickness in the O₃ and O₄ horizons. Average tree height was 27 m with a tree density of about 312 trees ha⁻¹ and a leaf area index of 7.2 (E. Falge, personnel communication). The understory was characterised by a closed cover dominated by the grasses Deschampsia flexuosa and Calamagrostis villosa, in large monospecific patches. Small patches of Urtica dioica and ‘nurseries’ of dense 2 to 4-yr-old P. abies patches also occur (Fig. 1).

2.2. Sampling system

To capture the temporal variation in CO₂ efflux on short (diurnal) and extended time scales (one growing season), a sampling system was constructed which was capable of continuously recording the instantaneous efflux rate from multiple sampling positions. Great care was taken in the construction of the sampling chambers to avoid measuring artefacts, in particular from pressure reductions in the chamber space which inherently cause problems with open chamber designs. Fig. 2 shows one open dynamic chamber installed at the site, showing the chamber design with air intakes of ambient and chamber air. A schematic diagram of the gas path between each of the five chambers and the gas analyser is shown in Fig. 3, while a more detailed description of the design and instrumental set-up can be found in Subke (2002).

The instantaneous soil CO₂ efflux from each of five chambers was measured sequentially once every hour. Chamber tests have shown that the presence of the chamber only slightly alters the temperature of the topsoil, and had no
discernible effect on the soil moisture (Subke, 2002). To avoid any artefact due to prolonged presence of the chamber, however, only readings of the instantaneous CO₂ efflux rate obtained within 24 h of positioning a chamber lid on a collar were considered valid data. Moving each of the five lids between the three collars of each measuring location (generally once every 1 to 3 d), allowed sufficient time for the environmental conditions within each collar to be unaffected by the previous presence of a chamber lid.

2.3. Installation of the soil respiration system in the field

Five sample locations within the stand were chosen for soil respiration measurements, and three collars were installed at each of these locations. Collars were inserted to a depth of between 1 and 2 cm into the soil, with about 50 cm spacing between collars at each location, and remained in place for the duration of the experiment. To capture potential differences in the soil CO₂ efflux due to the ground cover, two sampling locations were selected for each of the most dominant ground vegetation types, and a third location was located in a ‘nursery’ of 2-yr-old P. abies plants (Fig. 1). The chambers were usually positioned as far as possible from mature trees (between 3 and 4 m) with the exception of chamber 3, where the collars were within 0.5 and 1 m of a mature tree. Within each collar, all above-ground parts of the vegetation had been removed before

Fig. 2. Open dynamic soil chamber (design adapted from Rayment and Jarvis, 1997). Air is drawn from the chamber through the lateral canal, and ambient air passively follows the pressure gradient through the centrally mounted inlet tube. The intake of ambient air for the differential concentration measurements can be seen next to the inlet tube.

Fig. 3. Schematic diagram of the gas path between the five chambers and the infrared gas analyser (IRGA). A multiplexer controlled the switching of solenoid valves within the pumping unit (shaded area), thus directing the flow from the five chambers and a calibration line (top) sequentially to the IRGA. A datalogger (not shown) recorded all relevant readings at 1 min intervals.
measurements were made and any new growth removed during the season. Collars were installed 48h before measurements commenced to avoid artefacts due to the installation. Throughout this text, each of the 15 soil collars will be referred to according to the measuring location and the number of the collar within this location. For example, the collar description ‘5_2’ refers to the second collar of sampling location 5 (Fig. 1).

2.4. Soil respiration measurements

Readings of the differential CO2 concentration and the flow rate were obtained at 1 min intervals. The soil respiration rate could be calculated from the respective variables according to

\[ F_{\text{soil}} = \frac{C_{\text{diff}} k}{A}, \]

where \( C_{\text{diff}} \) is the differential CO2 concentration between chamber air and ambient (in \( \mu \text{mol mol}^{-1} \)), \( f \) is the flow rate (in \( \text{m}^3 \text{s}^{-1} \)), \( A \) is the chamber base area (315 cm^2), and \( k \) is a constant factor combining the conversions of CO2 concentrations from (\( \mu \text{mol mol}^{-1} \)) to (\( \mu \text{mol m}^{-3} \)) and for \( f \) from (\( \text{cm} \text{s}^{-1} \)) to (\( \text{m}^3 \text{s}^{-1} \)).

The CO2 differential signal was checked for stability to ensure steady-state conditions within the chamber, and the average value for the soil CO2 efflux of the last 3 min of a 10 min measuring interval were recorded.

2.5. Correlating measurements

The production of CO2 within the soil is basically a biochemical process and thus responds strongly to variations in temperature. This dependence may change with the age of the organic matter (roughly corresponding to increasing depth within the soil), and also with the availability of water for the relevant biochemical reactions. Accordingly, temperature probes and soil moisture sensors were installed near the soil collars. At each of the five locations, a temperature profile was sampled at 5, 10 and 30 cm depths once every 30 min. The soil water content (SWC) was recorded for the upper 10 cm of the organic layer (Theta Probes, Delta-T devices Ltd, Cambridge, UK). Since the variation in wind speed has been hypothesised to affect the transport of CO2 from the soil (Kimball and Lemon, 1971), wind velocity data, which was available from an eddy correlation sensor operated at the same site (Fig. 1), was also considered for analysis.

Measurements of SWC were not consistent throughout the year owing to the varying number of soil moisture probes used. To adjust an apparent bias due to the misrepresentation of the stand SWC by a too small number of probes, an existing stand process model was employed to simulate the water content of the organic layer. This process based model (PROXEL, Reichstein, 2001) includes a multi-layer soil compartment, in which the movement of water can be simulated. Using meteorological data that was available for the entire year and measurements of some soil qualities at the site, it was possible to simulate the organic SWC over 7 weeks for which good measurements (from five probes) were available. Since the data from the measuring probes was both discontinuous and inconsistent, only SWC values calculated using this model are used in the analysis.

2.6. Data analysis

2.6.1. CO2 efflux

The soil CO2 efflux was analysed with respect to its dependence on temperature (T), SWC, and wind forcing (u):

\[ F_{(\text{soil})} = f(T) \times f_{(\text{SWC})} + f(u). \]  

While T and SWC both act on the production of CO2 by autotrophic or heterotrophic respiration, \( u \) affects the physical transport of CO2 from the soil to the atmosphere. The amount emitted due to pressure induced pumping relates to a quantity of CO2 stored in the soil pores, which can be visualised as a buffer between the soil and the atmosphere that is depleted under turbulent and replenished under calm conditions, and the long-term average of this flux value is therefore zero. Accordingly, the dependence on wind induced pressure fluctuations is only used for instantaneous CO2 efflux measurements, while efflux averages are tested for \( T \) and SWC dependence only. Different possible relationships between the environmental variables and the CO2 efflux were tested for each of these functions (Sections 2.6.2–2.6.4). These are developed from existing equations, and the model parameters are estimated to fit the function to the measurement data using multivariate, non-linear regression. All regression fits were performed using the software PV-Wave version 6.21.

2.6.2. Temperature functions

The Arrhenius type function (Eq. (3)) as described by Lloyd and Taylor (1994) is widely accepted as a realistic description of the fundamental temperature dependence of soil respiration. The \( Q_{10} \) function (Eq. (4)) was used as an alternative exponential temperature relationship since it is also widely used. It is noted, however, that the concept of a strict \( Q_{10} \) relationship for soil respiration processes has been criticised on the basis of the variation of this factor itself with temperature and SWC (Howard and Howard, 1993; Lloyd and Taylor, 1994; Kutsch, 1996). The basic difference between these two functions is that in Eq. (3), the temperature sensitivity decreases with increasing temperature, while in Eq. (4), the relationship is constant throughout the temperature range. In order to assess the deviations of these relatively complex relationships from a simple linear one, a linear dependence of soil CO2 efflux on the soil temperature was also included (Eq. (5))

\[ f(T) = \frac{R_{\text{ref}}}{e^{F_T (1/56.02) - (1/T + 46.02)}}, \]  

\[ f_{(T)} = RT \times \exp \left( \frac{E_a}{T} \right) \]  

\[ f(T) = \frac{R_{\text{ref}}}{e^{F_T (1/56.02) - (1/T + 46.02)}}, \]
where $T$ is the soil temperature (in °C). All other model parameters were fitted by the multivariate non-linear regression. $R_{\text{ref}}$ is the soil respiration rate at the reference temperature $T_{\text{ref}}$ (here set to 10 °C, the median temperature of the data set), $E_0$ is an exponential parameter affecting the temperature sensitivity (which is related to the activation energy in the Arrhenius equation, see Lloyd and Taylor, 1994), and $m$ is the slope of the linear regression.

2.6.3. Soil water content functions

Soil CO$_2$ efflux data were not tested against the SWC alone, since this environmental variable shows less diurnal or seasonal variation than temperature, so that effects due to SWC would be masked by the influence of temperature. Instead, SWC sensitivity of soil CO$_2$ efflux was tested simultaneously to the temperature dependence by multiplying each of the $T$ functions with one of the SWC functions described in this section.

Eq. (6) is a modified version of the model proposed by Bunnell et al. (1977), while Eq. (7) is an alternative formulation derived from a Gompertz function after Janssens et al. (2002):

\[ f_{\text{SWC}} = \frac{\text{SWC}}{\text{SWC}_{1/2} + \text{SWC}}, \]  
\[ f_{\text{SWC}} = e^{-(\text{SWC}/\text{SWC}_{1/2})}, \]

where SWC is the volumetric soil water content (m$^3$ water m$^{-3}$ soil), SWC$_{1/2}$ is the soil water content, at which half the maximum respiration (i.e. under conditions without water stress at a given temperature) occurs, and $a$ and $b$ are both data set specific constants. Both the Bunnell and Gompertz model for soil water limitation included in their original form a constraint for limitation due to high SWCs. However, no meaningful parameters could be found for equations including soil CO$_2$ efflux limitation due to high SWCs, presumably owing to sufficient drainage of the upper soil layers at the Weidenbrunnen 2 site. Accordingly, Eqs. (6) and (7) only contain the functions describing limitations due to dry soil conditions.

2.6.4. Wind forcing function

Vertical movement of air may be induced by pressure differences that occur at the soil surface. This 'pumping' motion may represent a significant means of physical transport of CO$_2$ from the soil, and the open chamber design (in contrast to closed chamber models) allows this natural process to occur within the chamber space. The variation in wind speed ($c_\text{u}$) had been found to be an appropriate surrogate for pressure fluctuations (Subke, 2002). The function for wind forcing took the simple linear form of

\[ f_u = c\sigma_u \]  

where $\sigma_u$ is the standard deviation of the horizontal wind velocity (recorded at 20 Hz and aggregated into 1 s averages; standard deviations were formed for 10 min intervals for these 1 s averages) and $c$ is a linear parameter fitted during the regression routine.

2.7. Calculating the annual soil C efflux for Weidenbrunnen 2

The results of the data analysis described so far allow the calculation of soil CO$_2$ efflux rates for given environmental conditions. This allows the simulation of the soil CO$_2$ efflux for periods over which relevant input data are available but for which no measurements took place. It is thus possible to calculate efflux sums that can be compared either to the total stand flux of C, or for different periods to assess the temporal variability due to climatic variations.

The input for such a soil model created from the regression results is a continuous data set with all relevant environmental variables. The interest in this context is in long-term flux sums, so that the function influencing the transport of CO$_2$ ($f_u$) is of no relevance, since its average contribution to the efflux is zero (see Section 4 for more detail). For the remaining variables ($T$ and SWC), a long-term continuous data set could be constructed from a number of sources.

Soil temperature measurements form part of a measuring routine at an intensive research site immediately adjacent to the Weidenbrunnen 2 plot (data supplied by the Bayreuth Institute for Terrestrial Ecosystem Research, BITOK), and data were available from 1 April, 1997 to the 1 April, 2001. Following the results of the regression analysis, only the temperature at 5 cm depth was required, which was aggregated into hourly averages (from 10-min interval data). Short gaps in the data set (< 2 h) were filled by linear interpolation. For longer gaps (up to 36 h), the average was formed from the temperature readings taken at the same time of day on the preceding and following days and an approximation of a linear trend of the averaged values performed to maintain continuity. Following the described steps, most data gaps could be filled, but one longer period of missing data remained (8 August–12 September, 2000). Preliminary calculations showed that annual sums calculated from temperature data, aggregated into hourly averages, differed from sums calculated from data aggregated into daily averages by less than 0.2%. In order to simplify the gap filling of the remaining gap, data were aggregated into daily averages. It was possible to create a simple model based on (1) air temperature (also measured at an adjacent site and data supplied by BITOK), (2) the temperature at 5 cm depth averaged over the preceding 10 d, and (3) an approximation of the lower soil temperature. For the same periods in 1997–1999, this model produced calculated temperatures in good agreement with those measured (linear fit for measured vs. modelled temperatures: $r^2 = 0.91$, s.d. = 0.222, $n = 36$, $P < 0.0001$), so that a realistic modelling of the temperature at 5 cm depth for the period in 2000 can be assumed.
Comparison of the temperature measured in Weidenbrunnen 2 at 5 cm depth during this study, and the contemporary data from the Weidenbrunnen flux-tower site showed a good correlation ($r^2$ of 0.99 for daily averages for 145 d; data range: $<1$ to $>16^\circ$C). However, there was a consistent and significant ($P < 0.001$) deviation from the 1:1 line for the two temperature averages, possibly owing to a difference in stand structure or a slight difference in the burial depth of the respective temperature probes. For the modelling of soil CO$_2$ efflux from the Weidenbrunnen 2 site, the temperature readings from Weidenbrunnen were corrected according to $y = 0.878x + 1.31$.

Long-term data for the SWC of the organic layer were not available. However, using the model described for the derivation of SWC for 1999 (Reichstein, 2001), the SWC could be modelled from 1 April, 1997 to 31 March, 2001. Data gaps (due to missing precipitation data) never exceeded more than 7 d, and were filled using the seasonal average of previous and following years.

3. Results

3.1. Daily and seasonal patterns of soil CO$_2$ efflux

3.1.1. Seasonal and daily flux pattern

Soil respiration was measured continuously from 28 April to 3 December, 1999 with two long gaps in July and
September/October (2 and 4 weeks, respectively) due to instrument failure. The daily average soil CO₂ efflux rate (i.e. flux rates averaged for all collars measured in 1 d) ranged from 0.58 μmol m⁻² s⁻¹ on 16 November to 3.72 μmol m⁻² s⁻¹ on 26 July. The instantaneous CO₂ efflux rate could be as low as 0.43 μmol m⁻² s⁻¹ (17 November, collar 4_2) and as high as 5.15 μmol m⁻² s⁻¹ (on 19 July, collar 3_1). The range of the daily average CO₂ efflux rate varied between 0.24 and 2.59 μmol m⁻² s⁻¹ (on 15 November and 31 May, respectively), with greater variations occurring in summer when the efflux rate is greatest (Fig. 4). SWC limitation only occurred during short periods in summer, when the SWC dropped below 0.2 m³ m⁻³ in the organic layer, and the soil CO₂ efflux rate was reduced despite high soil temperatures.

Typical daily courses of the CO₂ efflux rates are plotted in Fig. 5, showing a marked increase from about 2 h after sunrise to about mid-afternoon and a slow decline throughout the night until the following morning. Soil CO₂ efflux rates usually peaked well after midday but before the maximum temperature at 5 cm depth was recorded. Daily time courses of CO₂ efflux were generally continuous but could show considerable variation between hourly readings (as, for example, on the afternoon of 20 August in Fig. 5). Flux measurements from all five collars collected within 1 h were aggregated, thus yielding a temporally and spatially averaged soil CO₂ efflux estimate. Since all chambers were moved between collars of a location simultaneously, the resulting averages represented three different spatial averages (for collars 1, 2, and 3 of all locations, respectively). Temperature regressions (using daily averages of CO₂ flux and temperature and Eq. (3)) for data obtained under conditions of no soil water limitation (see below) showed that the three spatial averages did not differ significantly from a regression using all data (χ² of grouped averages = 0.050, χ² of collar-averages = 0.072, 0.042 and 0.038, with n = 65, 23, 21 and 21, respectively), so that all flux averages could be treated as a true spatial average of the stand.

3.1.2. Temperature and soil water content dependence

Parameter fits were performed for the temperature dependence functions alone, as well as for all combinations of temperature and SWC functions

\[ F_{\text{soil}} = f_T f_{\text{SWC}}, \]

where \( f_T \) is one of Eqs. (3)–(5), and \( f_{\text{SWC}} \) takes the value 1 or is one of Eq. (6) or (7). Best fits of hourly flux-average data to Eqs. (3)–(5) were achieved for the soil temperature at 5 cm depth. All three temperature response functions fitted the data well, and multiplying each of the temperature functions by one of the SWC limitation functions improved the fit to the data (Table 1).

Out of all nine regression models indicated in Table 1, the combination of the Lloyd and Taylor (1994) temperature model and the SWC model after Bunnell et al. (1977) (Eqs. (3) and (6)) were chosen as for further data analysis, due to the slightly better value for the adjusted coefficient of correlation (adj. r²).

3.1.3. Interactions between the temperature and moisture dependence

The results presented in Table 1 clearly show the dependence of soil CO₂ efflux on the SWC. In order to test whether the temperature dependence of the CO₂ efflux in turn depends on the SWC, the hourly efflux averages were divided into SWC classes (between 0.20 and 0.32 m³ m⁻³, SWC classes had a width of 0.01 m³ m⁻³, above and below this range, classes contained a wider range of values to allow sufficient numbers of data points for regression
The effect of SWC limitation found for simultaneous regression of T Error bars are standard errors of the parameter estimation. Bunnell et al. (1977) (Eq. (6)) is also insensitive, whereas the parameter of the magnitude of the efflux and is temperature sensitive parameter shows no trend with both parameters against the different SWC classes, a clear sensitivity of the efflux to temperature changes. By plotting changing SWC (Fig. 6). The curve according to the SWC temperature and soil water content dependencies parameters and coefficients of determination for all combinations of

Temperature function

Lloyd and Taylor $Q_{10}$ Linear

<table>
<thead>
<tr>
<th>Moisture limitation function</th>
<th>Temperature function</th>
</tr>
</thead>
<tbody>
<tr>
<td>None $R_{ref}$</td>
<td>2.05 ± 0.01 2.03 ± 0.01 2.10 ± 0.01</td>
</tr>
<tr>
<td>$T$-par</td>
<td>304 ± 8 2.61 ± 0.07 0.199 ± 0.004</td>
</tr>
<tr>
<td>adj. $r^2$</td>
<td>0.72 0.70 0.74</td>
</tr>
<tr>
<td>Gompertz $R_{ref}$</td>
<td>2.65 ± 0.13 2.58 ± 0.11 2.60 ± 0.12</td>
</tr>
<tr>
<td>$T$-par</td>
<td>403 ± 8 3.64 ± 0.10 0.286 ± 0.015</td>
</tr>
<tr>
<td>$a$</td>
<td>0.364 ± 0.079 0.452 ± 0.086 0.167 ± 0.107</td>
</tr>
<tr>
<td>$b$</td>
<td>8.38 ± 1.13 8.09 ± 1.14 7.90 ± 1.45</td>
</tr>
<tr>
<td>adj. $r^2$</td>
<td>0.83 0.82 0.82</td>
</tr>
<tr>
<td>Bunnell $R_{ref}$</td>
<td>3.57 ± 0.13 3.66 ± 0.15 3.22 ± 0.10</td>
</tr>
<tr>
<td>$T$-par</td>
<td>403 ± 8 3.65 ± 0.10 0.355 ± 0.014</td>
</tr>
<tr>
<td>SWC$_{1/2}$</td>
<td>0.172 ± 0.015 0.188 ± 0.017 0.116 ± 0.010</td>
</tr>
<tr>
<td>adj. $r^2$</td>
<td>0.83 0.82 0.82</td>
</tr>
</tbody>
</table>

$T$-par refers to the respective parameters of the temperature sensitive parts of Eqs. (3)-(5), all other parameters are the same as for Eqs. (3)-(7). The coefficient of determination has been adjusted for the respective numbers of parameters; n = 822 for all regressions.

Table 1

Parameters and coefficients of determination for all combinations of temperature and soil water content dependencies

3.1.4. CO$_2$ soil efflux due to pressure pumping

The hypothesised influence of vertical air pumping on the CO$_2$ efflux from the soil acts only on the gas transport from the uppermost soil layer and not on the production of CO$_2$. Since the pressure fluctuations therefore only affect the instantaneous efflux situation, it was not deemed useful to average fluxes and environmental variables over any length of time. Best-fit regressions were applied to the instantaneous soil CO$_2$ efflux data for each collar separately. Only valid flux data for periods when wind-data was available were included. The regression model took the form of Eq. (2), with Eq. (3) for $f_T$, Eq. (6) for $f_{SWC}$ and Eq. (8) for $f_u$. In order to compare the effect of wind forcing on the efflux data, a second set of regressions were performed with $f_u$ set to zero. Variables used in the regression are the soil temperature at 5 cm depth and SWC of the organic layer for $T$ and SWC, respectively, and the standard deviation of the horizontal wind-speed 10 min previous to an efflux reading for $\sigma_u$.

As can be seen from Table 2, only about half of the chambers show a slight improvement in the value of the adjusted $r^2$ if $f_u$ is included (‘adj. $r^2(u)$’ compared to ‘adj. $r^2(u = 0)$’). Strikingly, all collars located in D. flexuosa patches (locations 3 and 4) show a better fit for regressions including the wind function, while most of the remaining collars show little or no improvement in the coefficient of determination. The value of $c$ was significantly different from zero for collars 3 and 4, suggesting that here an increased variability in wind speed is indeed positively correlated with the soil CO$_2$ efflux rate.

Fig. 6. Variations in the regression parameters $R_{ref}$ (triangles and left axis) for $T_{ref} = 10^\circ C$ and $E_0$ (circles and right axis) for different SWC classes. The line is the effect of SWC limitation found for simultaneous regression of $T$ and SWC (hatched grey line: $R_{ref} = 3.57 \times (SWC/SWC + 0.172)$; compare Table 1). Error bars are standard errors of the parameter estimation.
3.2. Spatial variation

Direct comparisons between soil respiration rates at different collars were not possible, since only five collars were measured simultaneously. In order to test for characteristic differences between the sampling locations, the instantaneous flux rate of CO₂ from each collar at between 9.5 and 10.5°C from the entire growing season (excluding periods when SWC became limiting) were compared. A total of 523 measurements had been conducted within this temperature range (between 80 and 121 for each of the locations), and no effect of hysteresis (i.e. whether temperature previous to the measurements had been either above or below the temperature range) was detectable.

CO₂ efflux rates of locations 1 and 3 were found to differ significantly from all other locations, and from each other (1-way ANOVA and Tukey test, F4500 = 92:1; P, 0:05), while locations 2, 4 and 5 show virtually identical rates. No significant difference due to the ground vegetation type (also indicated in Fig. 7) was apparent for data pooled for either collars or locations.

3.3. Annual soil CO₂ efflux for Weidenbrunnen 2

Fig. 8 shows the course of the soil temperature, SWC and the soil CO₂ efflux rate calculated using Eqs. (3) and (6) with the parameters stated in Table 1. The regression of all soil CO₂ efflux data obtained for SWC > 0.2 against Eq. (3) yielded the parameters Rref = 2.09 ± 0.01 and E₀ = 354 ± 8 (n = 702, adj. r² = 0.82). A comparison of the efflux modelled from the two regressions illustrates the effect of SWC limitation in the summer months (Fig. 9).

Based on the temperature and SWC regression results, the total soil CO₂ efflux over the 4-yr-period could be estimated. Given the extent of the available soil temperature data, annual totals were calculated from 1 April of each year to 31 March of the following year, and annual sums are given in Table 3.

According to the rainfall data supplied by BITÖK, 1997 was an extremely dry year. Comparison with rainfall sums recorded over 14-d intervals showed that while the annual precipitation sum was lower than in all previous and following years, technical problems with the rainfall instruments contributed to considerable underestimations of the annual total. The discrepancies between the hourly data (on which the SWC model is based) and the alternative fortnightly measurements occurred in winter and between late June and late July. During the 4 weeks between 26 June and 22 July, the SWC model under-estimated actual SWC by an equivalent of about 38 mm rainfall. The prolonged water stress indicated for the second half of 1997 (Fig. 8), however, is consistent with the 14-d interval rainfall data.
Fig. 7. Average soil respiration rates at around 10 °C of the five sampling locations. Error bars indicate 95% confidence intervals, means with the same letters are not significantly different (P = 0.05).

Fig. 8. Four year time course of (a) soil temperature (black line and left axis) and SWC (grey line and right axis), and (b) the modelled soil CO₂ efflux rate.
4. Discussion

4.1. Fundamental temperature dependence of soil CO₂ efflux

A positive relationship between soil temperature and soil CO₂ efflux rate is well established (Lundegårdh, 1926; Singh and Gupta, 1977; Raich and Schlesinger, 1992) and is clearly reflected in the seasonal course of both variables in Fig. 4. The causal link of this positive correlation by the increased biological activity of both the autotrophic (roots, e.g. Bouma et al., 1997) and the heterotrophic organisms (microbial communities and soil dwelling animals) in the soil and the increased diffusivity of CO₂ under higher temperatures is also undisputed. The exact nature of this relationship, however, is less clear and receives considerable attention (see Janssens et al., 2002 for a review). Of all existing empirical relationships, only three were tested on the data collected during this study These are (1) an Arrhenius type temperature response, (2) the \( Q_{10} \) concept, and (3) a simple linear regression.

The \( Q_{10} \) relationship expresses the factor by which a biochemical reaction increases when the temperature increases by 10 °C. The wide use of this purely empirical relationship in biological systems has been criticised by Lloyd and Taylor (1994) who point out that \( Q_{10} \) functions systematically overestimate fluxes at high temperatures. In the modified Arrhenius relationship for temperature and soil respiration proposed by Lloyd and Taylor, which was also used in this study, the activation energy decreases with increasing soil temperature. This soil respiration model (Eq. (3)) has since been supported by other researchers (Fang and Moncrieff, 1999; Rayment and Jarvis, 2000), but the \( Q_{10} \) concept is still widely used (Boone et al., 1998; Davidson et al., 1998; Mörén and Lindroth, 2000), in some cases alongside the Lloyd and Taylor-model (Fang et al., 1998; Buchmann, 2000). The regression results of both daily and hourly averages of soil CO₂ efflux obtained in this study (Table 1) support the Lloyd and Taylor model as the more realistic concept for soil CO₂ efflux measurements.

The apparent good fit of a linear regression model (Fig. 10) presumably stems from larger scatter at high soil temperatures, where all functions describe the data equally well, and the less represented measurements at low soil temperatures, where the linear model underestimates the measured efflux. Depending on soil types

Table 3

<table>
<thead>
<tr>
<th></th>
<th>Annual mean ( T ) (°C)</th>
<th>Precipitation (mm)</th>
<th>( T ) and SWC model (g C m (^{-2}) y (^{-1}))</th>
<th>( T ) only model (g C m (^{-2}) y (^{-1}))</th>
<th>‘T’-‘T&amp;SWC’ (g C m (^{-2}) y (^{-1}))</th>
<th>Over-estimate (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1997</td>
<td>5.9</td>
<td>572(^a)</td>
<td>497</td>
<td>588</td>
<td>91</td>
<td>15.5</td>
</tr>
<tr>
<td>1998</td>
<td>6.0</td>
<td>1300</td>
<td>566</td>
<td>581</td>
<td>15</td>
<td>2.6</td>
</tr>
<tr>
<td>1999</td>
<td>6.4</td>
<td>1170</td>
<td>592</td>
<td>602</td>
<td>10</td>
<td>1.5</td>
</tr>
<tr>
<td>2000</td>
<td>6.8</td>
<td>945</td>
<td>586</td>
<td>618</td>
<td>32</td>
<td>5.3</td>
</tr>
<tr>
<td>Mean ± st. dev.</td>
<td>6.0(^b)</td>
<td>1019(^b)</td>
<td>560 ± 43</td>
<td>597 ± 16</td>
<td>37 ± 37</td>
<td>6.2 ± 6.3</td>
</tr>
</tbody>
</table>

\(^a\) Precipitation data for 1997 likely to under-estimate actual precipitation sums; see text for detail.

\(^b\) Mean of the annual temperature and annual precipitation are calculated for the years 1993–2000 (data supplied by BITÖK).
and different temperatures investigated, linear regressions have been favoured to describe soil CO₂ efflux (Anderson, 1973; Koizumi et al., 1999). As with the $Q_{10}$ model, however, it lacks a physiological basis and bears obvious limitations for extrapolations within physiological scales, which is certainly desirable for modelling purposes. According to the parameters in Table 1, for example, soil respiration would become negative for temperatures below about $-1^\circ$C.

The presented soil CO₂ efflux data therefore show that the Lloyd and Taylor (1994) function, based on a temperature insensitive efflux rate at a set temperature ($R_{ref}$) and a parameter representing the activation energy ($E_0$) that varies according to the soil temperature, is the fundamentally soundest description of the relationship between soil temperature and soil CO₂ efflux. Therefore, only the Lloyd and Taylor function was used for the further analysis of the interaction between soil temperature and the soil CO₂ efflux.

### 4.2. Temperature profile within the soil

Of the factors influencing the soil respiration rate, soil temperature shows the greatest short-term variation. The surface efflux of CO₂ is the result of the heterotrophic and autotrophic activity from the entire soil profile, and depends on the substrate quality and the environmental conditions at all depths within this profile. The temperature within a given soil layer depends on the temperature in adjacent soil layers, air temperature and heating due to solar radiation. Greatest temperature fluctuations appear at the soil surface, due to seasonal and diurnal fluctuations in both radiation and air temperature. By means of thermal diffusion these fluctuations propagate to deeper soil layers, resulting in a more dampened and time-lagged temperature signal with increasing depth (Fig. 5). That the most shallow temperature sensor shows greatest diurnal variation is therefore obvious and clearly documented in Fig. 5. Since the organic layer with the greatest pool of easily decomposed C is hence exposed to the environmental variable with greatest fluctuation, the correlation between the CO₂ efflux rate and the most shallow soil temperature can be expected.

For the same forest plot, Buchmann (2000) found that removing the litter and organic layer of the forest floor (i.e. the top 13 cm of soil) led to no significant reduction in the soil CO₂ efflux rate, suggesting that the main source of CO₂ is located below these strata. Yet, the correlation between temperature and soil CO₂ efflux in the same study was less at 15 cm depth than it was at 10 or 5 cm depth ($r^2 = 0.70, 0.80$ and 0.80, respectively). The only meaningful interpretation of these apparently contradictory results in the same study is that the deeper soil layers contribute the bulk of CO₂ without any temperature sensitivity, and the more shallow layers contribute a small but changeable and temperature dependent portion of the CO₂ flux. However, looking at short-term variability of soil CO₂ efflux found in our study, peak efflux rates regularly exceed twice the nighttime values of within 24 h of measuring (data not shown, but see Fig. 5). This pattern indicates that a large fraction of the CO₂ flux originates in those soil strata that are affected by the diurnal temperature cycle (i.e. the litter and organic layer). The absence of a reduction in efflux after removal of these layers found by Buchmann (2000) is therefore likely to be attributed to measuring artefacts due to disturbance of the soil environment, and not a major contribution of the efflux from the mineral soil.

Mariko et al. (2000), Davidson et al. (2000) and others have pointed out the limitations of using a simple temperature function from one soil depth only to describe the process operating throughout the profile and is...
influenced by the heterogeneity of substrate and environmental factors. Splitting the temperature response function into several components to represent the flux contribution from different soil layers is one step towards a better understanding of the origin of CO₂ within the soil. However, this would increase the number of parameters in a regression model thus requiring more data points to yield a significant regression result (Draper and Smith, 1981, p. 298, recommend that the number of observations exceeds the number of parameters 5- to 10-fold). Soil respiration studies, especially those conducted using manually operated closed chambers, often do not provide sufficient numbers of observations to allow regressions of this kind. Despite sufficient amounts of data obtained in our study, it was not possible to extract information about compound fluxes from two different soil depths, and the temperature measured at a depth of 5 cm alone was found to be adequate for a description of the surface CO₂ flux. Closer analysis of the interactions of variables showed a high degree of correlation between the temperature signals from 5 and 10 cm depth ($r^2 = 0.85$, $P < 0.001$), resulting in these two temperatures to effectively act as one single variable. The correlation between the more shallow temperatures and the temperature at 30 cm depth was less, but including the deeper temperature for the modelling of the flux did not result in a significantly improved explanation of soil surface efflux variation.

However, there is evidence that the temperature closer to the soil surface, where the most extreme short-term changes in temperature due to changing direct and diffuse radiation take place, show even greater correlation with the efflux rate. The peak rates in Fig. 5 generally precede the peak of the soil temperature curve at 5 cm. The most extreme peaks are likely to result from times when the soil chamber was exposed to relatively high radiation and the temperature at the soil surface had increased considerably. Similar peaks were observed for all collars and at various times of the day. If one looks at measurements taken at the same collar over the course of several weeks, the limitations of using just one temperature for the correlation becomes evident. While an exponential regression gives a good fit for data of the entire growing season, the actual correlation for measurements taken within 24 h show a different dependence on soil temperature at 5 cm (Fig. 11a and b).

A likely cause for this difference between short- and long-term temperature dependence is the correlation of the efflux rate with the inappropriate temperature signal. That the temperature signal is dampened due to thermal inertia with increasing depth has already been shown. If one presumes that the short-term variability in the efflux rate is due to the temperature variation in the top-most layer alone, the correlating temperature signal from a deeper soil layer would have to be corrected for the signal-dampening. If the efflux rates in Fig. 11b were plotted against a broader temperature range, the daily temperature dependence curves would resemble the seasonal temperature dependence more closely. The magnitude of the flux, however, is still affected by temperatures from all depths, so that if one wanted to decrease the scattering around the annual regression line, a more detailed knowledge of the soil temperature distribution, especially at the soil surface would be necessary.

4.3. Soil moisture limitations

Limitation of soil CO₂ efflux due to either low or high SWCs have been described previously, and a multitude of regression models exist (Davidson et al., 2000; Janssens et al., 2002). Drought stress occurs as water becomes limiting for the normal metabolic activity of microbial organisms or macroflora (Singh and Gupta, 1977). At the opposite end of the optimal range for respiratory activity, a reduction due to high SWCs may occur as water limits the diffusion of gases in and out of soil pores. With no O₂ available for the aerobic decomposition process, CO₂ production is inhibited as well as its transport from the soil pores to the atmosphere (Linn and Doran, 1984). No limitation due to high SWC was observed at our site, probably owing to adequate drainage by the mineral soil (a sandy loam with a clay content of less than 5%). The limiting effect of low SWC however is pronounced, and

![Fig. 11](image-url)
the adequacy of the Bunnell model (Eq. (6)) for the
description is clearly documented in Fig. 6. Like most other
functions used to describe SWC limitations, this model is
empirically based. Papendick and Campbell (1981) show
that the mechanistically appropriate function scales the CO2
empirically based. Papendick and Campbell (1981) show
exact relationship between SWC and the soil CO2 efflux rate
model, with only one fitted parameter, was favoured. The
Gompertz model, so that in this study, the Bunnell
virtually identical results to those of both the Bunnell and
the Gompertz model, so that in this study, the Bunnell
model, with only one fitted parameter, was favoured. The
exact relationship between SWC and the soil CO2 efflux rate
differs from one soil type to another (Howard and Howard,
1993), and is also likely to depend on adaptations by the soil
microbial communities to local climatic conditions. Severe
soil CO2 efflux limitations in more arid ecosystems, for
example, do not occur until the SWC drops below about
0.1 m³ m⁻³ (Carlkyre and Ba Than, 1988; Janssens et al.,
2000, 2003). Since drought stress is not common at the
Weidenbrunnen 2 site, there is only minor environmental
pressure for microbial communities to develop appropriate
adaptations. The value of about 0.2 m³ m⁻³ for the
volumetric water content below which soil CO2 efflux
occurs is similar to those reported in other studies from
temperate and boreal regions of between 0.12 and
0.19 m³ m⁻³ (temperate deciduous; Hanson et al., 1993;
Armeth et al., 1998; Davidson et al., 1998; boreal coniferous:
Gårdenäs, 2000). The logarithmic regression model describing
soil water limitation of soil CO2 efflux in an Asian steppe ecosystem (Chen et al., 1999) indicates that similar
adaptation processes act in quite different ecosystem types.

Carlkyre and Ba Than (1988), Kutsch and Kappen (1997),
and Reichstein et al. (2002) have suggested a dependence of the
temperature sensitivity on SWC, a result that is not
supported by our findings. Since dry conditions usually
coincide with high soil temperatures, the effect of either
variable becomes confounded with the other (Davidson
et al., 1998). Given this dependence of variables, reduction
in temperature sensitivity may be due to an increase in
temperature (a well-established relationship, see above)
rather than the supposed soil moisture effect. Regressions
using the Arrhenius type model (which already incorporates
a decrease in temperature sensitivity with increasing
temperatures) showed for the data from Weidenbrunnen 2,
that the decrease in soil CO2 efflux can be explained purely
by a reduction in the (temperature insensitive) basal
respiration rate (Fig. 6). Moisture effects, on the other hand,
have also been observed on the E0-parameter, so that
further experimental work is needed in order to clarify this
particular effect.

4.4. Soil CO2 efflux facilitation by wind forcing

Measurements of the soil CO2 efflux are very sensitive to
atmospheric pressure, and that static pressure fluctuations
cause a mass flow in and out of the soil pores and hence
increase the rate of diffusion of a gas from the soil has been
shown experimentally by Kimball and Lemon (1971). Closed
chamber systems generally exclude these natural
fluctuations to occur within the chamber space, so that no
investigation into these effects has been reported from
studies using this chamber type alone. Rayment and Jarvis
(2000) who also used an open chamber design found no
improvement of the description of the efflux data by
including the friction velocity in their model. The only
evidence of wind-induced pressure pumping stems from
micrometeorological measurements of soil respiration
(Baldocchi and Meyers, 1991; Arnesth et al., 1998). Since
the causal mechanism of the mass flow in and out of the soil
pores is the variation in static air pressure, the direct use of
this variable is most desirable. Wind is the movement of air
due to gradients in air pressure, so that the variation in wind
speed (expressed as s) is a reasonable surrogate for static
pressure fluctuations (sp). Correlations between sp and the
friction velocity (u*; used as a surrogate by Rayment and
Jarvis (2000)) and between sp and u (as used by Arnesth
et al., 1998) were both weaker than for s (data not shown).

The effect of pressure pumping on the soil CO2 efflux is
likely to differ according to soil properties like soil bulk
density and soil pore sizes. Using the Bowen Ratio/Energy
Balance method and a closed dynamic soil chamber, Dugas
(1993) measured the CO2 flux from bare clay soil. The
reasonably good agreement between both methods with no
reported effect of wind speed indicates that the effect of
pressure pumping is negligible for this particular soil type.
For our data, an effect of pressure pumping could be
demonstrated for few of the 15 soil collars. However, there
appears to be a correlation between the type of ground
vegetation a collar was located in and the influence of static
pressure fluctuations: All six collars located in D. flexuosa
patches showed a higher coefficient of determination for the
remaining nine collars (Table 2). No aboveground parts
of the ground vegetation were present within the chambers,
but the litter and the O1 layer were strongly influenced by the
respective ground vegetation types. The thickness of the
litter layer in the D. flexuosa patches varies between 2 and
5 cm, compared to 1–1.4 cm for all other ground vegetation
patches. The bulk density of the litter layer was found to
range from 0.2 to 0.3 g cm⁻³ for all sites, which is
considerably less than that of the organic and mineral soil
(1.5 and 1.7 g cm⁻³, respectively). It is therefore plausible
that the effect of CO2 flushing from the soil pores due to
pressure fluctuations was only detected at those collars with
a more substantial layer of low bulk density (and hence a
greater pore volume).

The range of σu recorded was 0.04 to 1.35 m s⁻¹
(mean = 0.34, median = 0.30, n = 12 868), so that the
contribution of the pressure-induced efflux could be as large
as 1.17 μmol m⁻² s⁻¹ (by multiplying the maximum value of
σu by 0.869, the largest value for parameter c in Table 2).
However, it would be too simplistic to associate a given
value of σu with a specific flux contribution, since
the meteorological conditions previous to the measurement (on a scale of hours to days) would have to be accounted for first. The flux contribution due to pressure pumping is likely to be considerable for gusts of wind following a period of relative calm, while it should be smaller for similar given wind conditions if the soil pores have been 'flushed' by pumping previously.

For the purpose of modelling the long-term soil CO₂ efflux, however, it is not sensible to include pressure fluctuations as an additional variable, since it only affects the gas transport mechanism and not the CO₂ production within the soil. Averaged over time, therefore, the net contribution of the pressure related transport would be zero. However, our results show that measurements done by chambers that do not measure under steady-state conditions are likely to produce biased results owing to the present and previous meteorological conditions. Similarly meteorological techniques such as eddy covariance, which require minimum wind speeds and friction velocities to be applicable, would over-estimate soil CO₂ efflux, as only the ‘flushing’ of CO₂ from the soil would be recorded and not the relatively low efflux rate following times of high pressure fluctuations.

4.5. Annual soil CO₂ efflux

The calculated soil CO₂ efflux for the years 1997 to 2000 show considerable inter-annual variability (Table 3). During years when annual precipitation sums are close to the long-term average (as for the years 1998 to 2000), SWC limitation leads to a reduction of between 9 and 33 g C m⁻² yr⁻¹ (or about 1.5–5.5%) of the respiration sum under conditions without SWC limitation. If longer periods of SWC limitation occur, as in 1997, C loss from the soil is reduced considerably. While the values stated in Table 3 are likely to be an under-estimation of the annual rainfall, the severity of the SWC limitation on the annual soil CO₂ efflux is obvious. The annual results of about 570 g C m⁻² yr⁻¹ for the years 1998 to 2000 compare well to the 560 ± 17 g C m⁻² yr⁻¹ reported by Raich and Schlesinger (1992) for coniferous forests between 40 and 60° latitude. Buchmann (2000) calculated an annual efflux of 710 g C m⁻² yr⁻¹ for a neighbouring stand ‘Weidenbrunnen 1’ (a 47-yr-old dense plantation of P. abies) based on measurements from 1998, while the soil CO₂ efflux rates in Weidenbrunnen 2 were stated as even higher than in Weidenbrunnen 1, so that an even greater annual sum would result. The theoretical efflux rates reported by Buchmann with instantaneous flux rates of 1 μmol m⁻² s⁻¹ at 0 °C and about 5 μmol m⁻² s⁻¹ at 15 °C for the Weidenbrunnen 2 site do not compare well with those of our study (compare Figs. 2 and 8). The reason for the higher estimate by Buchmann (2000) may be partly explained by a misrepresentation of the actual stand soil CO₂ efflux due to a small number of sampling locations (in the mentioned study ‘four to five’ collars were used in the stand), or a systematic error of either of the sampling systems used. An intercomparison of chamber types conducted within the framework of the EUROFLUX programme (Lankreijer et al., 2003) showed that open dynamic chamber systems produce generally lower efflux estimates than closed dynamic systems. Given the intensive validation of the open dynamic chamber used in our study (Subke, 2002), and the higher total sampling area (4712 cm² = 314 cm² × 15 collars) in this study vs. 393 cm² (= 79 cm² × 5 collars) in Buchmann (2000), the lower estimate of around 580 g C m⁻² yr⁻¹ is likely to be a more accurate representation of the actual annual efflux.

In most temperate ecosystems, SWC limitation only occurs sporadically, and differs in frequency and duration between years (Fig. 8). Sampling strategies that rely on periodic measurements rather than continuous flux readings therefore run the risk of under-estimating the effect of SWC on soil CO₂ efflux, if short periods of low SWC are not sampled. The pronounced decrease in annual C loss from the soil for 1997 illustrates the necessity to incorporate the SWC sensitivity of soil CO₂ efflux into global change models. With global precipitation patterns changing along with regional annual mean temperatures, an estimate of future contributions to the total C budget by the soil is only possible if the SWC sensitivity is known and can be described mathematically.

4.6. Conclusion

The automated and continuous measurements with the open dynamic chamber system have provided a powerful basis for a comprehensive analysis into the factorial dependence of soil CO₂ efflux. The results provide detailed information that can be used to parameterise ecosystem models. Owing to the continuous soil CO₂ efflux data, periodic events such as sporadic drying of the top-soil were detected and the SWC limitation could be included in the mathematical description of the soil CO₂ efflux. The considerable inter-annual variability in the flux sums underlines the necessity to include the effect of the SWC in ecosystem models for humid as well as arid and semi-arid ecosystems.

At the same time, the results also show in which areas more research efforts have to be undertaken in order to understand the dynamics of the C balance of ecosystems. A simple extrapolation of the results would suggest that an increase in temperature would result in higher CO₂ production from the soil (assuming unchanged SWC conditions). However, if the amount of organic C available for microbial decomposition remains unchanged, the total amount of CO₂ efflux would remain constant. One study of old SOM in boreal soils (Liski, 1997), for example, found this particular fraction to be insensitive to temperature changes. A more thorough analysis of specific rates of decomposition for C pools of different stability within the soil would be needed in order to predict the likely behaviour of forest soils under a changed climate.
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