Summer drought reduces total and litter-derived soil CO\(_2\) effluxes in temperate grassland – clues from a \(^{13}\)C litter addition experiment

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Abstract. Current climate change models predict significant changes in rainfall patterns across Europe. To explore the effect of drought on soil CO\(_2\) efflux (\(F_{\text{Soil}}\)) and on the contribution of litter to \(F_{\text{Soil}}\), we used rain shelters to simulate a summer drought (May to July 2007) in an intensively managed grassland in Switzerland by reducing annual precipitation by around 30% similar to the hot and dry year 2003 in Central Europe. We added \(^{13}\)C-depleted as well as unlabelled grass/clover litter to quantify the litter-derived CO\(_2\) efflux (\(F_{\text{Litter}}\)). Soil CO\(_2\) efflux and the \(^{13}\)C/\(^{12}\)C isotope ratio (\(\delta^{13}\)C) of the respired CO\(_2\) after litter addition were measured during the growing season 2007. Drought significantly decreased \(F_{\text{Soil}}\) in our litter addition experiment by 59% and \(F_{\text{Litter}}\) by 81% during the drought period itself (May to July), indicating that drought had a stronger effect on the CO\(_2\) release from litter than on the belowground-derived CO\(_2\) efflux (\(F_{\text{BG}}\), i.e. soil organic matter (SOM) and root respiration). Despite large bursts in respired CO\(_2\) induced by the rewetting after prolonged drought, drought also reduced \(F_{\text{Soil}}\) and \(F_{\text{Litter}}\) during the entire \(^{13}\)C measurement period (April to October) by 26% and 37%, respectively. Overall, our findings show that drought decreased \(F_{\text{Soil}}\) and altered its seasonality and its sources. Thus, the C balance of temperate grassland soils respond sensitively to changes in precipitation, a factor that needs to be considered in regional models predicting the impact of climate change on ecosystems C balance.

1 Introduction

Current climate models predict a change of precipitation amounts and patterns throughout Europe. More precisely, one of the possible scenarios is an increasing frequency of summer droughts resulting in a reduction of plant available water (Meehl et al., 2007). The changes in precipitation will therefore affect terrestrial ecosystems, as precipitation is among the primary controls on ecosystem processes, e.g. net primary production (e.g. Knapp and Smith, 2001), N mineralization (e.g. Barnard et al., 2006), and soil respiration (e.g. Chou et al., 2008; Borken and Matzner, 2009).

Soil CO\(_2\) efflux (\(F_{\text{Soil}}\)) is one of the largest carbon fluxes between ecosystems and the atmosphere (Raich and Schlesinger, 1992), and the amount of carbon stored in soil is around three times greater than that in the atmosphere (Amundson, 2001). Within the terrestrial biosphere, grasslands cover around 40% of the ice-free global land surface (White et al., 2000) and a large fraction of their biomass is belowground. Therefore, grassland soils constitute relatively large organic carbon stocks and store globally around 28–37% of the terrestrial soil organic C pool (Lal, 2004). Hence, they play a critical role in the global carbon cycle. Furthermore, there is evidence that \(F_{\text{Soil}}\) from grasslands may be about 20% higher than from forests, because root activity, the quality and amounts of detritus as well as rates and mechanisms of decomposition differ between the two ecosystem types (Raich and Tufekcioglu, 2000).

Accurate estimates of \(F_{\text{Soil}}\) and its partial fluxes are still very challenging (Ryan and Law, 2005) and the response mechanisms to the impact of global change (e.g. drought)
on C cycling in temperate grasslands are not yet fully understood. In general, the effects of changes in precipitation amounts and patterns (e.g. Knapp et al., 2002; Chou et al., 2008) are not as well studied as those of increasing temperature (e.g. Luo, 2007) or rising atmospheric CO$_2$ concentrations (e.g. Luo et al., 2006). Furthermore, most climate manipulation studies in grasslands have focused on the response of aboveground C dynamics to changes in precipitation amounts and patterns (e.g. Knapp et al., 2002), instead of determining responses of the belowground system.

The effect of drought on $F_{\text{Soil}}$ may be either direct through changes in microbial activity and root respiration or indirect through altered supplies of substrates by rhizo-deposition and root turnover (Sowerby et al., 2008). Studies predominantly in wet or cold habitats reported that drought has resulted in increased rates of $F_{\text{Soil}}$ (e.g. Kim et al., 1992; Sowerby et al., 2008), while studies in mesic and drier habitats observed a reduction of $F_{\text{Soil}}$ due to increased plant and microbial stress (e.g. Bremer et al., 1998; Harper et al., 2005; Garten et al., 2009) as well as no or limited effects (Freeman et al., 1996). Furthermore, several sources (auto- and heterotrophic) contribute to $F_{\text{Soil}}$ with each of them probably responding differently to changes in precipitation amounts and patterns (Borken et al., 2006; Inglima et al., 2009). However, the partitioning of total $F_{\text{Soil}}$ into autotrophic (roots and rhizosphere) and heterotrophic respiration (micro-organisms decomposing litter ($F_{\text{Litter}}$) and soil organic matter) is remarkably difficult and thus represents still one of the greatest challenges in the research of the carbon cycle (Borken et al., 2006). Therefore, the contribution of decomposing litter to soil CO$_2$ efflux is still poorly known. Moreover, the complex and interactive effects of meteorological and environmental factors on $F_{\text{Soil}}$ complicate any prediction on how $F_{\text{Soil}}$ and $F_{\text{Litter}}$ would respond to drought. Thus, quantifying these two key processes in the carbon cycle is critical to accurately estimate the carbon budget of an ecosystem, and to better understand how soil C release responds to global change.

To investigate the effect of summer drought on $F_{\text{Soil}}$ and on the decomposition of fresh litter, we established a field experiment using rain shelters to simulate a summer drought in a temperate grassland and separated the litter- and belowground-derived components of $F_{\text{Soil}}$ by applying $^{13}$C-labelled litter. Our hypothesis was that $F_{\text{Soil}}$ would decrease due to reduced soil water contents ($\theta_V$) and that litter decomposition would respond particularly sensitively, because the litter lays directly on the soil surface and is thus more exposed to desiccation and temperature changes. With this study, we aimed at estimating (i) the mean annual soil CO$_2$ efflux of a temperate grassland after litter addition, (ii) the contribution of litter-derived CO$_2$ to total soil CO$_2$ efflux, (iii) the effect of drought on the different components of CO$_2$ effluxes from soil.

## 2 Materials and methods

### 2.1 Study site

The field experiment was established in June 2005 on a managed grassland at the ETH research station Chamau approximately 40 km southwest of Zurich, Switzerland (47°12’ N, 8°24’ E). The area is flat and situated at 400 m a.s.l. In 2007, the annual precipitation summed up to 1232 mm and the mean annual temperature was 10$°$C (data from a nearby meteorological station; Zeeman et al., 2009). Soils are moderately acidic loamy Cambisols (pH 5.3, 28.6% sand, 48.8% silt, 22.6% clay; WRB classification (FAO, 2006)) with 31.0±0.8 g kg$^{-1}$ $C_{\text{org}}$ and 3.4±0.1 g kg$^{-1}$ $N_{\text{total}}$ at 0–10 cm soil depth ($n=41$; soil data from Roth (2007); Table 1). The vegetation is a grass-clover mixture, dominated by perennial grasses (e.g. Lolium spp.) and legumes (e.g. Trifolium spp.).

The growing season at this site is typically from April to October. No farmyard manure was applied during the whole experiment.

### 2.2 Drought simulation

In 2005, we established three drought plots with reduced precipitation and three un-manipulated control plots separated by a 2 m wide buffer strip on an area of approximately 25 m × 25 m ($n=3$ per drought treatment). In each of the drought plots, we installed rain shelters (3 m × 3.5 m) from 2 May 2007 to 10 July 2007. The shelters are a construction of steel frames covered with plastic foil, which keeps precipitation off the drought plots and thus manipulates soil moisture (for detailed information see Gilgen and Buchmann, 2009). All measurements (e.g. $F_{\text{Soil}}$) were conducted in a core area (1 m × 2 m) in the centre of the plots.

### 2.3 Site parameters

Soil moisture ($\theta_V$), soil temperature ($T_S$), air temperature and precipitation were measured continuously (Gilgen and Buchmann, 2009). ECHO probes (EC-20 EC$\text{H}_2\text{O}$ sensors, Decagon Devices Inc., Pullman, WA, USA connected to a CR10X datalogger, Campbell Scientific, Logan, UT, USA) were installed in 2006 at 5, 15, and 30 cm soil depth to measure volumetric soil water content every 10 min in two control and two drought plots ($n=2$). In the same four plots, soil temperature at 5, 15, and 30 cm soil depth was logged every 10 min using temperature probes installed in 2006 ($n=2$). Based on these ten-minute values, we calculated hourly mean values of soil moisture and soil temperature. Air temperature at 2 m height and precipitation were measured at an adjacent meteorological station (HydroClip S3, Rotronic AG, Basserdorf, Switzerland and Type 10116, Toss GmbH, Potsdam, Germany; Zeeman et al., 2009).

We estimated the ambient annual litterfall of the site (control conditions) by collecting all loose litter with a vacuum cleaner from a randomly placed frame (40 cm × 40 cm; $n=16$)
after the six mowing events in 2007. The collected biomass was dried at 40°C for 120 hours and then weighed.

2.4 Labelled litter experiment and soil CO₂ efflux measurement

To separate the components of $F_{\text{Soil}}$ into the litter-derived component and $F_{\text{BG}}$ (SOM and root respiration), we divided each plot in two subplots. In the subplots, we either added $^{13}$C-depleted (−37.2±0.1‰ (V-PDB)) or reference litter (−27.9±0.1‰ (V-PDB)), both mixtures of Lolium perenne and Trifolium repens collected in a previous free air carbon dioxide enrichment study (Hebeisen et al., 1997). In 2005, we permanently installed 12 thin-walled polyvinyl chloride collars (diameter 20 cm, 5 cm height, 3 cm inserted in the soil) to measure the soil CO₂ efflux (one collar per subplot). On 22 April 2007, we applied approximately 700 g m⁻² of dry biomass (equivalent to 165% of ambient annual litterfall (424 g m⁻²)) directly on the soil surface in the 12 respiration collars. We placed a 4 mm mesh size net on the collars to prevent wind dispersion and mixing with additional litterfall.

The measurements of soil CO₂ effluxes and air sampling for isotopic analysis have previously been described in Joos et al. (2008), thus, we only give a brief overview of the sampling procedure. Soil CO₂ efflux was measured using a soil CO₂ flux system (LI-8100, Li-Cor Inc., Lincoln, NE, USA). To measure $F_{\text{Soil}}$ and collect air samples simultaneously, we modified the chamber by adding a second collar with 5 replaceable septa (diameter 20 cm, 10 cm height) on top of the 12 permanently installed PVC collars (total V of chamber + collars = 8656.5 cm³). In total, we performed 26 CO₂ efflux measurement campaigns between April and December 2007 (for each campaign $n=3$) and 13 soil air sampling campaigns between April and October 2007 (for each campaign $n=3$), i.e. every two to four weeks. Measurements were carried out between 11:00 h and 18:00 h. To reduce plant respiration, we removed the aboveground vegetation down to 3 cm above ground level approximately 24 h before measurements.

2.5 Isotope analysis of respired CO₂ and calculation of litter-derived CO₂

To estimate the $\delta^{13}$C of soil resired CO₂, we collected five soil air samples during 15 min with syringes (Plastipak syringe and 27G×1” needle, Becton Dickinson, Fraga, Spain) out of the head space of the chamber connected to the portable soil CO₂ flux system and injected the sampled air into previously evacuated special glass vials (12 mL ex- etainer gas testing vials, capped with airtight rubber septa, cat. #738W; Labco Ltd., High Wycombe, UK; $n=5$ per subplot). For all $\delta^{13}$C analyses, the air samples were transferred from the vials with an autosampler (CombiPAL, CTC Analytics AG, Zwingen, Switzerland) in the helium gas stream to an automated online purification and pre-concentration system (Gasbench II; ThermoFinnigan MAT, Bremen, Germany), which was linked to an isotope ratio mass spectrometer (DeltaPlus XL, ThermoFinnigan MAT) for the determination of $\delta^{13}$C. The $\delta^{13}$C values of CO₂ are reported in the delta notation and referenced to the international V-PDB standard. The repeated measurement precision was ±0.02–0.03‰.

Isotopic signatures of soil gas samples represent a mixture of respired CO₂ and atmospheric CO₂. To estimate the $\delta^{13}$C values of the respired CO₂, we applied the so-called Keeling plot approach (Pataki et al., 2003) by regressing $\delta^{13}$C versus 1/CO₂ concentration. The resulting y-intercept represents the $\delta^{13}$C of the respiratory CO₂ source (Keeling, 1958). Least squares regression yielded always $R^2 > 0.95$. Our measurements and the calculation of the Keeling plots have previously been described in Joos et al. (2008).

For the partitioning of soil CO₂ efflux we estimated the $\delta^{13}$C of the respired CO₂ of subplots with $^{13}$C-depleted and reference litter. We calculated the contribution of fresh litter to soil CO₂ efflux ($F_{\text{Litter}}/F_{\text{Soil}}$) by a single isotope linear mixing model based on mass conservation equations (Balesdent et al., 1987):

$$F_{\text{Soil}} = F_{\text{Litter}} + F_{\text{BG}},$$

(1)

$$F_{\text{Litter}}/F_{\text{Soil}} = (\delta - \delta_{\text{BG}})/ (\delta_{\text{Litter}} - \delta_{\text{BG}}),$$

(2)

where $F_{\text{Soil}}$ is the total soil CO₂ efflux and $\delta$ is the isotopic composition of soil CO₂ estimated with Keeling plots. The mixing model is based on the two end-members, $\delta_{\text{Litter}}$ (isotopic composition of litter-respired CO₂) and $\delta_{\text{BG}}$ (isotopic composition of belowground CO₂ including CO₂ originating from root and SOM decomposition): $F_{\text{Litter}}$ and $F_{\text{BG}}$ are the associated fluxes. We used the isotopic composition of the litter for the $\delta_{\text{Litter}}$ values, assuming no discrimination during litter decomposition (subscripts $R$ for reference and $D$.

<table>
<thead>
<tr>
<th>Soil type¹</th>
<th>Cambisol</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sand (g kg⁻¹)²</td>
<td>306±52 (2)</td>
</tr>
<tr>
<td>Silt (g kg⁻¹)³</td>
<td>477±25 (2)</td>
</tr>
<tr>
<td>Clay (g kg⁻¹)⁴</td>
<td>217±27 (2)</td>
</tr>
<tr>
<td>Bulk density (g cm⁻³)</td>
<td>1.1±0.0 (41)</td>
</tr>
<tr>
<td>pH value</td>
<td>5.3±0.0 (2)</td>
</tr>
<tr>
<td>$C_{\text{org}}$ (g kg⁻¹)</td>
<td>31.0±0.8 (41)</td>
</tr>
<tr>
<td>$N_{\text{total}}$ (g kg⁻¹)</td>
<td>3.4±0.1 (41)</td>
</tr>
<tr>
<td>C/N</td>
<td>9.4±0.1 (41)</td>
</tr>
<tr>
<td>$C_{\text{org}}$ stock (t ha⁻¹)</td>
<td>32.9±2.2 (41)</td>
</tr>
</tbody>
</table>

¹ Classified after WRB Classification (FAO, 2006).
² <2000–63 μm.
³ >63–2 μm.
⁴ <2 μm.

Table 1. Soil properties of topsoil 0–10 cm (means±standard errors; $n=2$ and 41 are shown in brackets; Roth, 2007).
for $^{13}$C-depleted litter; Ngao et al., 2005). We estimated $\delta_{BG}$ by applying Eq. (2) for both $^{13}$C-litter treatments, assuming that there are no priming effects and thus no differences of $F_{\text{Litter}}/F_{\text{Soil}}$ between both treatments:

$$F_{\text{Litter}}/F_{\text{Soil}} = (\delta_D - \delta_{BGD})/(\delta_{LitterD} - \delta_{BGD}) = (\delta_R - \delta_{BGR})/(\delta_{LitterR} - \delta_{BGR}).$$

(3)

We solved Eq. (4) assuming that belowground CO$_2$ evolving from processes other than litter decomposition has the same isotopic composition in both $^{13}$C-litter treatments:

$$\delta_{BG} = (\delta_R \delta_{LitterD} - \delta_D \delta_{LitterR})/(\delta_R + \delta_{LitterD} - \delta_D - \delta_{LitterR}).$$

(4)

We estimated the isotopic compositions of respired CO$_2$ ($\delta_R$ and $\delta_D$) with the Keeling plot approach as described above (subscripts $R$ for reference and $D$ for $^{13}$C-depleted litter).

To estimate the fluxes of total litter-derived CO$_2$, we multiplied $F_{\text{Litter}}/F_{\text{Soil}}$ values with the measured soil CO$_2$ efflux.

### 2.6 Data analysis, model description, and flux estimates

We tested the differences of soil- ($F_{\text{Soil}}$), litter- ($F_{\text{Litter}}$) and belowground-derived CO$_2$ efflux values ($F_{BG}$) between drought and control plots using two-way ANOVA with the main factors sampling date and drought treatment (R Development Core Team, 2005). We used a reduced data set ($n=25$ for control and drought plots, respectively) to investigate the relationships of $F_{\text{Soil}}$, $F_{\text{Litter}}$ and $F_{BG}$ with $T_S$ and $\theta_V$ by eliminating the two peak values (control plots DOY 128, drought plots DOY 193) as they resulted mainly from processes other than litter decomposition or mineralization of lysed microbial biomass on the drought plots. The temperature dependency of soil CO$_2$ effluxes was estimated by fitting measured fluxes to the function of Lloyd and Taylor (1994):

$$F_{\text{Soil}} = a \cdot \exp(b + Ts),$$

(5)

where $a$ and $b$ are fitted constants.

The Lloyd and Taylor function was also used to calculate $Q_{10}$ values for drought and control plots. To ascertain the relationships between soil CO$_2$ effluxes and $\theta_V$ at 30 cm depth, we used negative quadratic functions according to Mielnick and Dugas (2000):

$$F_{\text{Soil}} = c \cdot \theta_V^2 + d \cdot \theta_V - f,$$

(6)

with $c$, $d$, and $f$ as fitted constants.

Furthermore, we assessed interactive effects of $T_S$ at 5 cm and $\theta_V$ at 30 cm depth on soil CO$_2$ effluxes by regressing them to a combination of the temperature and moisture functions.

Cumulated soil CO$_2$ effluxes were estimated by linearly interpolating the fluxes between the biweekly measurements except for the end of the drought period where we used the low values during the drought until the first rainfall. For the mean annual soil CO$_2$ effluxes, we used Eq. (5) to estimate the CO$_2$ fluxes for the periods before and after the CO$_2$ measurement period (DOY 1–92 and 343–365) and added them to the linearly interpolated values.

### 3 Results

#### 3.1 Drought simulation

The simulation of drought with rain shelters during 69 days between 2 May 2007 and 10 July 2007 effectively decreased the amount of ambient precipitation (1232 mm yr$^{-1}$) by around 400 mm (Fig. 1). As a consequence the drought treatment decreased the soil water content at 30 cm depth ($\theta_V$) in the drought plots by around 70% during the drought period, with a maximum relative decrease of approximately 76%. After the drought, it took two weeks until the soil water contents in the drought plots reached levels as in the control plots again. Thereafter, soil moisture at all depths remained approximately the same as in the control plots (except from DOY 269 to 299; Fig. 1). Soil temperature at 5 cm depth was not significantly affected by the drought treatment (Fig. 1).

#### 3.2 Soil CO$_2$ efflux

In the control plots, $F_{\text{Soil}}$ followed a seasonal trend during our litter addition experiment, with a very high peak (18 µmol m$^{-2}$ s$^{-1}$) shortly after the application of litter at the beginning of the growing season (Fig. 1). Afterwards, $F_{\text{Soil}}$ rapidly declined and levelled off to around 4 µmol m$^{-2}$ s$^{-1}$ during the summer before decreasing continuously until winter. Under control conditions, soil temperature ($T_S$) was the main driver of $F_{\text{Soil}}$, 44% of flux variability was explained by the Lloyd and Taylor function ($R^2=0.44$, $P < 0.001$, $n=25$; Table 2). For the entire CO$_2$ measurement period, the $Q_{10}$ value was 1.8. The relationship with soil moisture ($\theta_V$) as single factor was not significant. Mean annual soil CO$_2$ efflux from the control plots estimated by simple linear interpolation combined with the model calibrated against measured data from this experiment ($T_S$) for the winter values was 1.61 kg C m$^{-2}$ yr$^{-1}$ in 2007.

#### 3.3 Litter-derived soil CO$_2$ efflux

The addition of $^{13}$C-depleted litter was clearly reflected in the decrease of $\delta^{13}$C of respired CO$_2$ indicating that litter decomposition contributed significantly to soil CO$_2$ efflux. In the control plots, the litter-derived CO$_2$ efflux ($F_{Litter}$) peaked directly after litter addition (DOY 129) and declined exponentially with time. $F_{Litter}$ was below the detection limit 141 days after the litter addition (DOY 253; Figs. 2 and 3). Under control conditions, soil moisture ($\theta_V$) was the main driver of $F_{Litter}$. 70% of flux variability was explained by the negative quadratic function ($R^2=0.70$, $P < 0.001$, $n=12$; Table 2). The relationship with soil temperature ($T_S$) as single factor was not significant, and thus, it was not possible
Fig. 1. Precipitation, soil moisture at 15 and 30 cm depth, soil temperature at 5 cm depth and soil CO$_2$ efflux measured in drought and control plots during a litter addition experiment in 2007. Means and standard errors for soil CO$_2$ effluxes of three plots.

Fig. 2. $\delta^{13}$C values of soil CO$_2$ efflux for control and for drought plots and proportion of litter-derived CO$_2$ from the total soil CO$_2$ efflux in per cent for drought and control plots during a litter addition experiment in 2007. Means and standard errors of three plots.

Fig. 3. Litter- and belowground-derived CO$_2$ efflux ($F_{\text{Litter}}$ and $F_{\text{BG}}$) during a litter addition experiment in 2007. Means and standard errors of three plots.

to determine the temperature sensitivity. The combination of $T_S$ and $\theta_V$ improved the regression model significantly ($R^2=0.84$, $P<0.001$, $n=12$; Table 2). Between April and October 2007 the cumulative sums of $F_{\text{Soil}}$ and $F_{\text{Litter}}$ in the control plots were 1.29 kg C m$^{-2}$ and 0.27 kg C m$^{-2}$ respectively, yielding an average $F_{\text{Litter}}/F_{\text{Soil}}$ of around 21%. The total $F_{\text{Litter}}$ corresponded to 76% of the freshly applied litter C (0.35 kg C m$^{-2}$; Table 3).

3.4 Effects of drought on soil and litter-derived CO$_2$ efflux

The experimental drought significantly decreased the soil CO$_2$ efflux ($F_{\text{Soil}}$) after litter addition by 59% during the drought period ($P<0.05$), by 26% over the $^{13}$CO$_2$ measurement period ($P<0.05$; Fig. 1 and Tables 3 and 4), and by 19% during the whole year ($-330$ g C m$^{-2}$ yr$^{-1}$). Also in the drought plots, soil temperature ($T_S$) at 5 cm depth explained most of the variability of $F_{\text{Soil}}$ (45%; $R^2=0.45$, $P<0.001$, $n=20$) over the entire $^{13}$CO$_2$ measurement period. Despite the significant effect of drought, there was no significant relationship between $F_{\text{Soil}}$ and soil moisture ($\theta_V$) at any depth.
Table 2. Relationships of soil-, litter- and belowground-derived CO2 effluxes (\(F_{\text{Soil}}, F_{\text{Litter}}\) and \(F_{\text{BG}}\), respectively) to soil temperature at 5 cm (\(T_S\)) and soil moisture at 30 cm depth (\(\theta_V\)) (regression coefficients and temperature sensitivity coefficient (\(Q_{10} = e^{(b \cdot d)}\)). The CO2 measurement period data was only used between DOY 116–294 with 20 measurement dates for \(F_{\text{Soil}}\). The measurements of \(F_{\text{Litter}}\) and \(F_{\text{BG}}\) were conducted for 179 days (DOY 117–295; \(n=12\)). Best fits are indicated with bold letters.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Total Adjusted (R^2)</th>
<th>Control Drought</th>
<th>Control Drought</th>
</tr>
</thead>
<tbody>
<tr>
<td>(F_{\text{Soil}})</td>
<td>(T_S)</td>
<td>0.46***</td>
<td>0.44***</td>
</tr>
<tr>
<td>(\theta_V)</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>(T_S + \theta_V)</td>
<td>0.52***</td>
<td>0.67***</td>
<td>0.59***</td>
</tr>
<tr>
<td>(F_{\text{Litter}})</td>
<td>(T_S)</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>(\theta_V)</td>
<td>n.s.</td>
<td>0.70***</td>
<td>0.17*</td>
</tr>
<tr>
<td>(T_S + \theta_V)</td>
<td>0.12*</td>
<td>0.84***</td>
<td>0.27**</td>
</tr>
<tr>
<td>(F_{\text{BG}})</td>
<td>(T_S)</td>
<td>0.40***</td>
<td>0.40**</td>
</tr>
<tr>
<td>(\theta_V)</td>
<td>0.21**</td>
<td>0.39**</td>
<td></td>
</tr>
<tr>
<td>(T_S + \theta_V)</td>
<td>0.56***</td>
<td>0.70***</td>
<td>0.65***</td>
</tr>
</tbody>
</table>

Formulas: \(T_S = a \cdot \exp(b \cdot T_S)\)
\[\theta_V = a \cdot \theta_V^2 + d \cdot \theta_V - f\]
\[T_S + \theta_V = a \cdot \exp(b \cdot T_S) \left(c \cdot \theta_V^2 + d \cdot \theta_V - f\right)\]

Significance codes: \(P < 0.001***; 0.001 < P < 0.05**; 0.05 < P < 0.1*; P > 0.1 = \text{n.s.}\)

n.d.=not determinable.

(Table 2). However, the combination of \(T_S\) and \(\theta_V\) improved the regression model (\(R^2=0.59, P < 0.001, n=20\); Table 2).

The litter-derived CO2 efflux (\(F_{\text{Litter}}\)) under drought did not show the pronounced peak as in the control directly after litter application and it dropped close to zero towards the end of the drought (Fig. 3). The contribution of fresh litter to total soil CO2 efflux (\(F_{\text{Litter}}/F_{\text{Soil}}\)) in the drought plots also showed a different pattern than in the control plots. The values dropped immediately after the start of the drought treatment from 48% in early spring to 4% during the drought, indicating that \(F_{\text{Litter}}\) responded more sensitively to drought than total \(F_{\text{Soil}}\). The ratio of \(F_{\text{Litter}}/F_{\text{Soil}}\) started to rise again after the drought and reached a second peak value of 40% in August (Fig. 2). Subsequently, \(F_{\text{Litter}}/F_{\text{Soil}}\) declined and remained on a level of around 10% until the end of the experiment. The average \(F_{\text{Litter}}/F_{\text{Soil}}\) ratio was strongly reduced during the drought period itself (from 30% in the control plots to 16% in the drought plots, \(P=0.16\)), although we were not able to determine a significant effect. It was also not significantly affected by the drought treatment over the entire \(^{13}\)C measurement period (21% in the control plots; 18% in the drought plots, \(P=0.72\)). The drought treatment reduced the amount of litter-derived CO2 during the drought period by 81% compared to the control (\(P < 0.05\); Fig. 3, and Tables 3 and 4). Over the entire \(^{13}\)C measurement period from April to October 2007, the drought decreased the litter-derived CO2 efflux by 0.09 kg C m\(^{-2}\) yr\(^{-1}\), which corresponds to a 37% decrease compared to the control (\(P=0.33\)). Under drought, \(F_{\text{Litter}}\) was less closely related to soil moisture than under ambient conditions (Table 2).

4 Discussion

4.1 Soil CO2 efflux

The seasonal pattern of soil CO2 effluxes under control conditions showed a clear peak in mid May, which can be attributed to the high rates of litter decomposition at the first rainfalls after adding the litter (Fig 1). Thereafter, \(F_{\text{Soil}}\) decreased throughout the rest of the year as a result of a declining availability of easily-degradable litter components (Fig. 3) and decreasing temperatures in fall. Soil moisture had a small effect on \(F_{\text{Soil}}\) under ambient precipitation (Table 2). Rainfalls were evenly distributed across the seasons and hence, soil moisture varied little and was in the optimal range for soil respiration (20 to 40%; Mielnick and Dugas, 2000). Consequently, soil temperature was the main driver for \(F_{\text{Soil}}\) (Table 2) although the temperature dependency was superimposed by the litter addition.

The estimated mean annual soil CO2 efflux under control conditions after litter addition of 1.6 kg C m\(^{-2}\) yr\(^{-1}\) is in agreement with fluxes estimated by Bahn et al. (2008) for an Austrian grassland site under similar climatic conditions. They estimated a total annual soil respiration with natural litterfall of around 1.8 kg C m\(^{-2}\) yr\(^{-1}\). Both estimates are amongst the highest reported fluxes for terrestrial ecosystems. Our flux rates are supported by a high ecosystem respiration (2.5 kg C m\(^{-2}\) yr\(^{-1}\)) measured by eddy-covariance on the same grassland site nearby our study area (with farmyard manure application; Zeeman et al., 2009). We assume that the high \(F_{\text{Soil}}\) rates are not only related to the
Table 3. Effects of drought on grassland soil CO\(_2\) efflux during the litter addition experiment. The total cumulated sums of linearly interpolated mean flux rates as well as drought induced relative changes in \(F_{\text{Soil}}\), \(F_{\text{Litter}}/F_{\text{Soil}}\), \(F_{\text{Litter}}\) and \(F_{\text{BG}}\) are shown for the drought period (69 days) and the entire \(^{13}\)C measurement period (179 days) in 2007. Diff. (%): percentage difference between control and drought (Diff. (%)=(Drought-Control)/Control\(\times100\)).

<table>
<thead>
<tr>
<th></th>
<th>Drought period (DOY 122–191)</th>
<th>13(^{13})C measurement period (DOY 117–295)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Control</td>
<td>Drought</td>
</tr>
<tr>
<td>(F_{\text{Soil}}) (g C m(^{-2}))</td>
<td>620</td>
<td>257</td>
</tr>
<tr>
<td>(F_{\text{Litter}}) (g C m(^{-2}))</td>
<td>206</td>
<td>40</td>
</tr>
<tr>
<td>(F_{\text{Litter}}/F_{\text{Soil}}) (%)</td>
<td>30</td>
<td>16</td>
</tr>
<tr>
<td>(F_{\text{BG}}) (g C m(^{-2}))</td>
<td>414</td>
<td>217</td>
</tr>
</tbody>
</table>

Significance codes: \(P < 0.001***; 0.001 < P < 0.05**; 0.05 < P < 0.1\ *. 

Table 4. Statistical significance of \(F_{\text{Soil}}\), \(F_{\text{Litter}}\), \(F_{\text{Litter}}/F_{\text{Soil}}\), \(F_{\text{BG}}\) and \(F_{\text{BG}}/F_{\text{Soil}}\) during the drought period (69 days) and the entire \(^{13}\)C measurement period (179 days) in 2007. Degrees of freedom (\(df\)), F- and P-values from two-way ANOVA are shown (factors: sampling date and drought treatment).

<table>
<thead>
<tr>
<th></th>
<th>Drought period (DOY 122–191)</th>
<th>13(^{13})C measurement period (DOY 117–295)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(df)</td>
<td>(F)</td>
</tr>
<tr>
<td>(F_{\text{Soil}}) Sampling date</td>
<td>4</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>Drought treatment</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>4</td>
</tr>
<tr>
<td>(F_{\text{Litter}}) Sampling date</td>
<td>4</td>
<td>2.8</td>
</tr>
<tr>
<td></td>
<td>Drought treatment</td>
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</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>4</td>
</tr>
<tr>
<td>(F_{\text{Litter}}/F_{\text{Soil}}) Sampling date</td>
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<td>7.6</td>
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<tr>
<td></td>
<td>Drought treatment</td>
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</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>4</td>
</tr>
<tr>
<td>(F_{\text{BG}}) Sampling date</td>
<td>4</td>
<td>1.6</td>
</tr>
<tr>
<td></td>
<td>Drought treatment</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>4</td>
</tr>
</tbody>
</table>

4.2 Partitioning of soil CO\(_2\) efflux

To our knowledge this is the first study quantifying the contribution of litter to soil CO\(_2\) efflux (\(F_{\text{Litter}}/F_{\text{Soil}}\)) using \(^{13}\)C-depleted litter in grasslands. Most of the earlier experiments estimating the contribution of litter to total soil CO\(_2\) efflux (\(F_{\text{Soil}}\)) were litter manipulations in forest ecosystems (i.e., plots with and plots without litter). In our case, the litter-derived CO\(_2\) efflux (\(F_{\text{Litter}}\)) declined exponentially from April to October and amounted to approximately 0.27 kg C m\(^{-2}\)yr\(^{-1}\), corresponding to 21% of \(F_{\text{Soil}}\) and 76% of the freshly applied litter (Table 3). The \(^{13}\)C-tracer based estimate is in agreement with the litter mass loss in an accompanying litterbag study, where 86±4% (\(n=4\)) of the placed biomass had been lost during 138 days after litter placement on DOY 251 (data not shown). The contribution of litter-derived CO\(_2\) were similar to the 14 to 20% estimated for temperate tallgrass-prairies in a \(^{14}\)C-labelling experiment by Buyanovsky et al. (1987) and in a clipping study by Wan and Luo (2003). All these values for grassland soils were higher than the 10% reported for forest soils (e.g. Bowden et al., 1993; Maier and Kress, 2000), very likely reflecting...
the higher decomposability of grass litter. Assuming that the autotrophic component contributes to one-third to \( F_{\text{Soil}} \) (mean value of 25 temperate grassland studies reviewed by Wang and Fang, 2009), \( F_{\text{Litter}} \) would correspond to about 25% of the heterotrophic part of \( F_{\text{Soil}} \).

Our results show that the two components of \( F_{\text{Soil}} \) were affected differently by climatic factors under ambient precipitation. While the litter-derived \( CO_2 \) efflux was mainly controlled by soil moisture (\( R^2=0.70 \)), the belowground component was equally driven by soil temperature and soil moisture (\( R^2=0.40 \) and \( R^2=0.39 \), respectively; Table 2). The likely reason for the different response of the two components of \( F_{\text{Soil}} \) is that the litter layer dried out more rapidly than the mineral soil and thus, litter decomposition – in contrast to SOM mineralisation in the deeper soil – was temporarily limited by moisture.

### 4.3 Effects of drought

The applied experimental drought in this study reduced summer precipitation by around 30%, similar to the natural drought across Central Europe in 2003 and the model predictions for Northern Europe (Ciais et al., 2005). The rainfall removal by the roofs induced a drought in the plant and soil system. Volumetric soil moisture at 30 cm was reduced from 40% under ambient precipitation to 10% under drought (Fig. 1). Plant productivity, photosynthesis as well as leaf water potentials also declined substantially (Gilgen and Buchmann, 2009; Signarbieux, 2009). As 80% of the roots are typically in the uppermost 30 cm depth (Jackson et al., 1996; Bessler et al., 2009) and most of the \( CO_2 \) production occurs in the uppermost 10 cm of a Swiss grassland soils under similar site conditions (Flechard et al., 2007), we assume that the experimental drought affected the major part of the biologically active soil.

Our results clearly indicated a more sensitive response of \( F_{\text{Litter}} \) to drought than of \( F_{\text{BG}} \) (Fig. 3), which supports the greater moisture sensitivity of the litter-derived \( CO_2 \) efflux under ambient precipitation (Table 2). These findings are in agreement with the study of Theis et al. (2007) in an alpine grassland which showed that during the drought period of 2003 the \( CO_2 \) efflux from litter and top soil horizons were close to zero through the desiccation of these layers. \( F_{\text{Soil}} \) was obviously originating from the deeper soil horizons with different temperature and moisture regimes, a similar situation as in our drought experiment. The consequences of a suppressed litter and an ongoing C mineralisation in the deeper soil is a stronger loss of older soil carbon under drought. Our results support the conclusion by Davidson et al. (2004) that for the adequate assessment of soil respiration, the variation in the depth where the \( CO_2 \) is produced needs to be known and thus soil moisture and \( CO_2 \) production must be measured or modelled depthwise.

The experimental drought did not decrease the temperature sensitivity of total soil \( CO_2 \) efflux (Table 2) which contrasts with the compilation of soil respiration data from different ecosystems by Reichstein et al. (2003). One reason for the apparently lacking change in the temperature sensitivity is the overarching effect of the litter addition on \( F_{\text{Soil}} \). Moreover, the increase in soil \( CO_2 \) effluxes occurred delayed which hampered a direct comparison to ambient conditions.

Microbial respiration is strongly driven by \( T_s \) and \( \theta_V \) and is minimized or even ceases during drought (Wang et al., 2003). In our study, \( F_{\text{Litter}} \) was almost negligible towards the end of the drought period (Fig. 3). We measured a large respiration pulse at the first rain events after simulated drought, which is in agreement with the so-called “Birch-effect”, a large burst of litter mineralization immediately after rewetting (Birch, 1958; Fierer and Schimel, 2003; Harper et al., 2005). These pulses of high \( F_{\text{Soil}} \) may be the result of an increased availability of labile organic substrates through microbial death and cell lysis (Halverson et al., 2000) or through destabilization of soil aggregates (Denef et al., 2001). In our study, the delayed litter decomposition under drought and thus remaining labile litter most probably also contributed to the \( CO_2 \) flush in the drought plots after the end of the drought treatment (Fig. 2).

Previous studies have indicated that the water status of an ecosystem influences the direction of its response to drought and rewetting. In wet soils, drought has resulted in an increase of \( F_{\text{Soil}} \) (Kim et al., 1992; Davidson et al., 2004; Sowerby et al., 2008), while for mesic and drier habitats reduced \( F_{\text{Soil}} \) or negligible drought effects have been observed (Freeman et al., 1996; Bremer et al., 1998; Harper et al., 2005; Garten et al., 2009). Beside the short-term effects during the drought period itself, we also observed a significant reduction of cumulated \( F_{\text{Soil}} \) over the entire \( ^{13}CO_2 \) measurement period by 26% from April until October (Tables 3 and 4). Harper et al. (2005) suggested that drought affects \( F_{\text{Soil}} \) by reducing the substrate supply and/or the microbial populations. As we added the same amount of substrate on each plot, differences in substrate supply can be excluded as an explanation. The reduction of \( F_{\text{Soil}} \) could also be in part a result of plant responses to drought, e.g. reduction in C assimilation (Knapp et al., 2002), reduction in root mass (Johnson and Matchett, 2001) and lower root respiration (Rochette et al., 1991). In our study, the experimental drought decreased plant aboveground biomass productivity in 2007 by 27% (Gilgen and Buchmann, 2009). However, belowground biomass production did not respond to the drought indicating that the allocation of resources to roots was similar under control and drought conditions. In turn, this suggests that the reduced \( F_{\text{BG}} \) during drought can be mainly attributed to a decreased heterotrophic respiration, which is in agreement with the findings of Borken et al. (2006) that prolonged summer drought in forest soils primarily reduced the respiration losses of radiocarbon-old \( CO_2 \).

Drought reduced the litter-derived soil \( CO_2 \) efflux (\( F_{\text{Litter}} \)) significantly for the drought period (69 days; Fig. 2, Table 3). The peak of \( F_{\text{Litter}} \) after rewetting was, however, less
pronounced than the observed value for total soil CO$_2$ efflux (Figs. 1 and 3), possibly because the real CO$_2$ flush from the litter was missed by the biweekly measurements. Despite increasing $F_{\text{litter}}$ after the drought, drought decreased the total litter-derived CO$_2$ efflux and the ratio of $F_{\text{litter}}/F_{\text{Soil}}$ for the entire $^{13}$C measurement period (Table 3) but it is not clear, if the measurement period in our study was long enough to capture the full effect of a prolonged drought on the microbial activity. Hence, it is possible that the temporarily reduced $F_{\text{Soil}}$ might get compensated later through a delayed decomposition of labile components and/or a retarded priming (Subke et al., 2006). However, rewetting experiments in the laboratory by Muhr et al. (2008) suggest that CO$_2$ production without litter addition quickly recovers back to the same level as permanently wet soil independent on the intensity of the previous drought. We therefore assume, that also on an annual basis drought will reduce soil CO$_2$ effluxes with the litter component being more affected than the belowground one.

Net ecosystem exchange measurements by Ciais et al. (2005) and Scott et al. (2009) suggest that forests and semiarid grasslands turn into a CO$_2$ source with increasing summer droughts. Our study suggests a negligible drought effect on the net C balance of the grassland as the drought reduced the annual soil CO$_2$ effluxes and total biomass production by about 300 to 350 g C m$^{-2}$ yr$^{-1}$ (Table 3; Gilgen and Buchmann, 2009). The long-term effect remains unknown as a declining plant productivity will also reduce the litter inputs into soils and thus, soil CO$_2$ effluxes.

5 Conclusions

Simulated summer drought significantly reduced soil CO$_2$ efflux rates and altered its seasonality, showing that grassland soils are highly sensitive to changes in soil moisture. The partitioning of soil CO$_2$ efflux using $^{13}$C-depleted litter in a litter addition experiment indicated that drought significantly affected the sources of soil-respired CO$_2$ with a stronger effect on the contribution of litter- than of belowground-derived CO$_2$. Despite a CO$_2$ flush at rewetting - the so-called “Birch-effect” – the reduction in $F_{\text{Soil}}$ during drought was not fully compensated over the entire $^{13}$C measurement period (179 days). Thus, our findings indicate that drought caused C losses from soils during one growing season. However, these losses were balanced out by a similar reduction in plant productivity, suggesting that the net effect of the drought on ecosystems C balance was negligible.

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References


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