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**Summer drought
reduces total and
litter-derived soil CO₂
effluxes in grassland**

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Summer drought reduces total and litter-derived soil CO₂ effluxes in temperate grassland – clues from a ¹³C 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 CO₂ efflux (F_{Soil}) and on the contribution of litter to F_{Soil} we used rainout shelters to simulate a summer drought (May to July 2007) in an intensively managed grassland in Switzerland, and to reduce annual precipitation by around 30% similar to the hot and dry year 2003 in Central Europe. We added ¹³C-depleted as well as unlabelled grass/clover litter to quantify the litter-derived CO₂ efflux (F_{Litter}). Soil CO₂ efflux and the ¹³C/¹²C isotope ratio ($\delta^{13}\text{C}$) of the respired CO₂ after litter addition were measured during the growing season 2007. Drought significantly decreased F_{Soil} in our litter addition experiment by 52% and F_{Litter} by 74% during the drought period itself (May to July), indicating that drought had a stronger effect on the CO₂ release from litter than on the belowground-derived CO₂ efflux (F_{BG} , i.e. soil organic matter (SOM) and root respiration). Despite large bursts in respired CO₂ induced by the rewetting after prolonged drought, drought also reduced F_{Soil} and F_{Litter} during the entire ¹³C measurement period (April to October) by 32% and 33%, respectively. Overall our findings highlight i) the sensitivity of temperate grassland soils to changes in precipitation, a factor that needs to be considered in regional models predicting the impact of climate change, and ii) the need to quantify the response of the different components of soil CO₂ efflux to fully understand climate change impacts on ecosystem carbon 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 amounts of precipitation will therefore affect terrestrial ecosystems, as precipitation is among the primary controls on ecosystem pro-

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cesses, e.g. net primary production (e.g. Knapp and Smith, 2001), N mineralization (e.g. Barnard et al., 2006) and soil respiration (e.g. Lai et al., 2003; Chou et al., 2008).

Soil CO₂ efflux (F_{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 two to 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 (C_{org}) 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 soil CO₂ efflux (F_{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_{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) are not as well studied as those of increasing temperature (e.g. Luo, 2007) or rising atmospheric CO₂ concentrations (e.g. Luo et al., 2006). Furthermore, most climate manipulation studies in grasslands have focused on the responses 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_{Soil} may be either direct through changes in microbial activity and root respiration or indirect through altered supplies of substrates by rhizodeposition and root turnover (Sowerby et al., 2008). Studies predominantly in wet or cold habitats reported that drought has resulted in increased rates of F_{Soil} (e.g. Kim et al., 1992; Sowerby et al., 2008), while studies in mesic and drier habitats observed a reduction of F_{Soil} due to increased plant and microbial stress (e.g. Bremer et al.,

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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_{Soil} with each of them probably responding differently to changes in precipitation amounts and patterns (Inglisma et al., 2009). However, the partitioning of total F_{Soil} into autotrophic (roots and rhizosphere) and heterotrophic respiration (micro-organisms decomposing litter (F_{Litter}) and soil organic matter) is remarkably difficult and thus represents still one of the greatest challenges in the research of the carbon cycle (Baggs, 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_{Soil} complicate any prediction on how F_{Soil} and F_{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_{Soil} and on the decomposition of fresh litter, we established a field experiment using rainout shelters to simulate a summer drought in a temperate grassland and separated the litter-derived and belowground component of F_{Soil} by applying ^{13}C -labelled litter. Our hypothesis was that F_{Soil} would decrease due to reduced soil water contents (Θ_V) and that litter decomposition would respond particularly sensitive, 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 total and litter-derived CO_2 efflux rates from soil.

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2 Materials and methods

2.1 Study site

The field experiment was established in June 2005 on 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 $31.0 \pm 0.8 \text{ g kg}^{-1} \text{ C}_{\text{org}}$ and $3.4 \pm 0.1 \text{ g kg}^{-1} \text{ N}_{\text{total}}$ 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 unmanipulated control plots separated by a 2 m wide buffer strip on an area of approximately 25×25 m ($n=3$ per drought treatment). In each of the drought plots, we installed rainout shelters (3×3.5 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_{Soil}) were conducted in a core area (1×2 m) in the centre of the plots.

2.3 Site parameters

Soil moisture (Θ_V), soil temperature (T_S), air temperature and precipitation were measured continuously (Gilgen and Buchmann, 2009). ECHO probes (EC-20 ECH₂O sen-

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sors, Decagon Devices Inc., Pullman, WA, USA connected to a CR10X datalogger, Campbell Scientific, Logan, UT, USA) were installed in 2006 at approximately 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 10-min 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 (40×40 cm; $n=16$) after the six mowing events in 2007. The collected biomass was dried at 40°C for 120 h and then weighed.

2.4 Soil CO₂ efflux and labelling experiment

To separate the components of F_{Soil} into the litter-derived component and F_{BG} (SOM and root respiration), we divided each plot in two subplots. In the subplots, we either added ¹³C-depleted ($-37.2 \pm 0.1\%$ (V-PDB)) or reference litter ($-27.9 \pm 0.1\%$ (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 and air sampling procedures have been previously described in Joos et al. (2008), thus, we only give a brief overview of the sampling proce-

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5 dure. Soil CO₂ efflux was measured using a soil CO₂ flux system (LI-8100, Li-Cor Inc., Lincoln, NE, USA). To measure F_{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 done between 11:00 h and 18:00 h. To reduce plant respiration, we removed the aboveground vegetation down to 3 cm above
10 ground level approximately 24 h before measurements.

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

To estimate the $\delta^{13}\text{C}$ of soil respired 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
15 CO₂ flux system and injected the sampled air into previously evacuated special glass vials (12 mL exetainer gas testing vials, capped with airtight rubber septa, cat. #738W; Labco Ltd., High Wycombe, UK; $n=5$ per subplot). For all $\delta^{13}\text{C}$ 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, Ger-
20 many), which was linked to an isotope ratio mass spectrometer (Delta^{Plus} XL, ThermoFinnigan MAT) for the determination of $\delta^{13}\text{C}$. The $\delta^{13}\text{C}$ values of CO₂ are reported in the delta notation and referenced to the international V-PDB standard. The repeated measurement precision was $\pm 0.02\text{--}0.03\text{‰}$.

25 Isotopic signatures of soil gas samples represent a mixture of respired CO₂ and atmospheric CO₂. To estimate the $\delta^{13}\text{C}$ values of the respired CO₂, we applied the so-called Keeling plot approach (Pataki et al., 2003). We took 5 gas samples within

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a 15 min sampling period and calculated Keeling plots by regressing $\delta^{13}\text{C}$ versus $1/\text{CO}_2$ concentration. The resulting y-intercept represents the $\delta^{13}\text{C}$ of the respiratory CO₂ source (Keeling, 1958). Ohlsson et al. (2005) have demonstrated the possibility to use least squares regression (LSR) for high R^2 of Keeling plots ($R^2 > 0.95$). Thus, we performed our Keeling plots with LSR, because our results always had $R^2 > 0.95$. Our measurements and the calculation of the Keeling plots have been previously described in Joos et al. (2008).

For the partitioning of soil CO₂ efflux we estimated the $\delta^{13}\text{C}$ of the respired CO₂ of subplots with ¹³C-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; Cheng, 1996; Rochette et al., 1999; Hanson et al., 2000):

$$F_{\text{Soil}} = F_{\text{Litter}} + F_{\text{BG}} \quad (1)$$

$$F_{\text{Litter}}/F_{\text{Soil}} = (\delta - \delta_{\text{BG}})/(\delta_{\text{Litter}} - \delta_{\text{BG}}) \quad (2)$$

where F_{Soil} is the total soil CO₂ efflux and δ is the isotopic composition of soil CO₂ estimated with Keeling plots. The mixing model is based on the two end-members, δ_{Litter} (isotopic composition of litter-respired CO₂) and δ_{BG} (isotopic composition of belowground CO₂ including CO₂ originating from root and SOM decomposition): F_{Litter} and F_{BG} are the associated fluxes. We used the isotopic composition of the litter for the δ_{Litter} values, assuming no discrimination during litter decomposition (subscripts R for reference and D for ¹³C-depleted litter; Ngao et al., 2005). We estimated δ_{BG} by applying Eq. (2) for both ¹³C-litter treatments, assuming that there are no priming effects and thus no differences of $F_{\text{Litter}}/F_{\text{Soil}}$ between both treatments:

$$\begin{aligned} F_{\text{Litter}}/F_{\text{Soil}} &= (\delta_{\text{D}} - \delta_{\text{BGD}})/(\delta_{\text{LitterD}} - \delta_{\text{BGD}}) \\ &= (\delta_{\text{R}} - \delta_{\text{BGR}})/(\delta_{\text{LitterR}} - \delta_{\text{BGR}}) \end{aligned} \quad (3)$$

We solved Eq. (4) assuming that belowground CO₂ evolving from processes other than litter decomposition has the same isotopic composition in both ¹³C-litter treatments:

$$\delta_{BG} = (\delta_R \delta_{LitterD} - \delta_D \delta_{LitterR}) / (\delta_R + \delta_{LitterD} - \delta_D - \delta_{LitterR}). \quad (4)$$

We estimated the isotopic compositions of respired CO₂ (δ_R and δ_D) with the Keeling plot approach as described above (subscripts R for reference and D for ¹³C-depleted litter).

To estimate the fluxes of total litter-derived CO₂, we calculated daily F_{Litter}/F_{Soil} values by interpolating linearly between the mean values of each of the 13 ¹³CO₂ efflux measurements, then we calculated daily F_{Litter} values by multiplying the interpolated F_{Litter}/F_{Soil} with the corresponding interpolated F_{Soil} value. Finally, we summed up all daily F_{Soil} , F_{BG} and F_{Litter} values between April and October 2007.

2.6 Data analysis, model description and gap filling

We tested the differences of soil- (F_{Soil}), litter- (F_{Litter}) and belowground-derived CO₂ 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_{Soil} , F_{Litter} and F_{BG} with T_S and Θ_V by eliminating the two peak values (control plots DOY 128, drought plots DOY 193) as they resulted mainly from the application of the dried litter and from delayed litter decomposition or mineralization of lysed microbial biomass on the drought plots. Small gaps in our T_S and Θ_V data sets that resulted from technical problems (e.g. gaps of 9 d for T_S in the control plots and 97 d for Θ_V in the drought plots) were filled by linear regressions, e.g. between soil temperatures of drought and control plots ($T_{SControl} = 1.0034 * T_{SDrought} + 1.075$; $R^2 = 0.98$, $P < 0.001$) and between soil water contents of different depths for drought and control plots ($\Theta_{VDrought 5cm} = 1.0756 * \Theta_{VDrought 15cm} + 1.044$; $R^2 = 0.54$, $P < 0.001$). We included

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all 26 soil CO₂ efflux values of the control plots (including the above mentioned peak value) and corresponding T_S ($n=26$ for control plots) for the model parameterisation of the following model for F_{Soil} (Lloyd and Taylor, 1994):

$$F_{\text{Soil}} = a * \exp(b * T_S), \quad (5)$$

where a and b are fitted constants.

For the estimates of soil CO₂ effluxes during the CO₂ measurement period, we linearly interpolated the fluxes between the biweekly measurements. For the mean annual soil CO₂ effluxes, we used Eq. (5) to estimate the CO₂ fluxes for the periods before and after the CO₂ measurement period (DOY 1–92 and 343–365) and combined them with the linearly interpolated values. The Lloyd and Taylor function was also used to assess the effect of drought on the temperature sensitivity of soil CO₂ effluxes by calculating Q_{10} values for drought and control plots. To ascertain the relationships between soil CO₂ effluxes and Θ_V at 5 cm depth, we used negative quadratic functions according to Mielnick and Dugas (2000): ($F_{\text{Soil}} = c * \Theta_V^2 + d * \Theta_V - f$; with c , d , and f as fitted constants). Furthermore, we assessed interactive effects of T_S and Θ_V at 5 cm depth on soil CO₂ effluxes by regressing them to a combination of the temperature and moisture functions.

3 Results

3.1 Drought simulation

The simulation of drought with rainout shelters during 69 d between 2 May 2007 and 10 July 2007 effectively decreased the amount of ambient precipitation (1232 mm yr⁻¹) by around 400 mm (Fig. 1a). As a consequence the drought treatment decreased the soil water content (Θ_V) in the drought plots by around 20–60% during the drought period, with a maximum relative decrease of approximately 83%. After the drought, it took two weeks until the soil water contents in the droughtplots reached levels as in the control

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plots again. From then on, soil moisture at 5 cm depth remained approximately the same as in the control plots (except from DOY 269 to 299; Fig. 1b). Soil temperature at 5 cm depth was not significantly affected by the drought treatment (Fig. 1c).

3.2 Soil CO₂ efflux

5 In the control plots, F_{Soil} followed a seasonal trend during our litter addition experiment, with a very large peak ($18 \mu\text{mol m}^{-2} \text{s}^{-1}$) shortly after the application of litter at the beginning of the growing season (Fig. 1d). After this peak, F_{Soil} rapidly declined and levelled off to around $4 \mu\text{mol m}^{-2} \text{s}^{-1}$ during the summer before decreasing continuously until winter. Under control conditions, soil temperature (T_{S}) was the main driver of F_{Soil} , 42% of flux variability was explained by the exponential function (adjusted $R^2=0.42$, $P<0.001$, $n=25$; Table 2). We estimated a Q_{10} value of 3.3 for the entire CO₂ measurement period. The relationship with soil moisture (Θ_{V}) as single factor was not significant (adjusted $R^2=0.01$, $P=0.30$, $n=25$). Mean annual soil CO₂ efflux from the control plots estimated by simple linear interpolation combined with the model calibrated against measured data from this experiment (T_{S}) was $1.70 \text{ kg C m}^{-2} \text{ yr}^{-1}$ in 15 2007 (Table 3).

3.3 Litter-derived soil CO₂ efflux

The addition of ¹³C-depleted litter was clearly reflected in the decrease of $\delta^{13}\text{C}$ of respired CO₂, indicating that litter decomposition contributed significantly to soil CO₂ efflux (Fig. 2). In the control plots, the litter-derived CO₂ efflux (F_{Litter}) peaked directly after litter addition (DOY 129) and declined exponentially with time (Fig. 3). F_{Litter} was below the detection limit 141 d after the litter addition (DOY 253; Figs. 2a and 3). Between April and October 2007 the cumulative sums of F_{Soil} and F_{Litter} in the control plots were 1.43 kg C m⁻² and 0.27 kg C m⁻², respectively, yielding an average $F_{\text{Litter}}/F_{\text{Soil}}$ of around 20 19%. The total F_{Litter} corresponded to 76% of the freshly applied litter C (0.35 kg C m^{-2}); 25

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Table 4).

3.4 Effects of drought on soil and litter-derived CO₂ efflux

The experimental drought significantly decreased the soil CO₂ efflux (F_{Soil}) after litter addition by 52% during the drought period ($P < 0.001$) and by 22% over the entire CO₂ measurement period ($P < 0.05$; Fig. 1d and Tables 3 and 5). Although we found a reduced temperature sensitivity ($Q_{10} = 2.8$ vs. 3.3), soil temperature (T_S) at 5 cm depth was still the most important driver of F_{Soil} accounting for approximately 45% of flux variability (adjusted $R^2 = 0.45$, $P < 0.001$, $n = 25$) in the drought plots over the entire CO₂ measurement period. Despite the significant effect of drought, soil moisture (Θ_V) at 5 cm depth was not a significant driver (adjusted $R^2 = -0.03$, $P = 0.6$, $n = 25$). However, the incorporation of T_S and Θ_V improved the regression model (adjusted $R^2 = 0.56$, $P < 0.001$, $n = 25$; Table 2).

The litter-derived CO₂ efflux (F_{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. 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_{Litter} responded more sensitive to drought than total F_{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. 2c). 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, $P < 0.05$), but was not significantly affected by the drought treatment over the entire ¹³C measurement period (19% in the control plots; 18% in the drought plots, $P = 0.5$). The drought treatment reduced the amount of litter-derived CO₂ during the drought period by 74% compared to the control ($P < 0.001$; Fig. 3, and Tables 4 and 5). Over the entire ¹³C measurement period from

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April to October 2007, the drought decreased the litter-derived CO₂ efflux by 0.09 kg C m⁻², which corresponds to a 33% decrease compared to the control ($P=0.001$).

4 Discussion

4.1 Soil CO₂ efflux

5 Under control conditions our estimate of mean annual soil CO₂ efflux after litter addition ($F_{\text{Soil}}=1.7 \text{ kg C m}^{-2} \text{ yr}^{-1}$; from linear interpolation combined with the model; Table 3) 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 $1.8 \text{ kg C m}^{-2} \text{ yr}^{-1}$. Both estimates are amongst the highest
10 reported fluxes for terrestrial ecosystems so far. Our flux rates are supported by a high ecosystem respiration ($2.5 \text{ kg C m}^{-2} \text{ yr}^{-1}$) measured by eddy-covariance on the same grassland site (but with farmyard manure application) nearby our study area (Zeeman et al., 2009). We assume that the high F_{Soil} rates are not only related to the litter we applied (around 165% of annual litterfall), because we avoided the common farmyard
15 manure application (app. $0.4 \text{ kg C m}^{-2} \text{ yr}^{-1}$ in 2007; Zeeman et al., 2009) and natural litterfall in our plots. Thus, the total annual input of carbon was even less than under natural field conditions. Therefore, it seems more likely that the high F_{Soil} rates reflect the high productivity of Swiss grasslands driven by high summer soil temperatures combined with almost optimal soil moisture (Bahn et al., 2008).

20 4.2 Partitioning of soil CO₂ efflux

To our knowledge this is the first study quantifying the contribution of litter to soil CO₂ efflux ($F_{\text{Litter}}/F_{\text{Soil}}$) using ¹³C-depleted litter in grasslands. Most of the earlier experiments estimating the contribution of litter to total soil CO₂ efflux (F_{Soil}) were litter manipulations in forest ecosystems (i.e. plots with and plots without litter). In our case,

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the litter-derived CO₂ efflux (F_{Litter}) from April to October amounted to approximately 0.27 kg C m⁻², corresponding to 19% of F_{Soil} and 76% of the freshly applied litter (Table 4). The ¹³C-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 d after litter placement on DOY 251 (data not shown). Our estimate of $F_{\text{Litter}}/F_{\text{Soil}}$ for grassland was well within the range of 14 to 20% in temperate grasslands (e.g. Buyanovsky et al., 1987; Wan and Luo, 2003) and higher than the values reported for forest soils of about 10% (e.g. Bowden et al., 1993; Maier and Kress, 2000). Assuming that the autotrophic component contributes to one-third to F_{Soil} (mean value of 25 temperate grassland studies, review by Wang and Fang, 2009), F_{Litter} would correspond to about 25% of the heterotrophic part of F_{Soil} .

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). Our results clearly indicated a more sensitive response of F_{Litter} to drought than of F_{BG} (Fig. 3). This is in agreement with the study of Theis et al. (2007) in an alpine grassland who showed that during the drought period of 2003 the CO₂ efflux from litter and top soil horizons were close to zero through the desiccation of these layers. F_{Soil} was obviously originating from the deeper soil horizons with different temperature and moisture regimes, a similar situation as in our drought experiment.

Microbial respiration is strongly driven by T_{S} and Θ_{V} and is minimized or even ceases during drought (Wang et al., 2003). In our study, F_{Litter} was almost negligible towards the end of the drought period (Fig. 3a). 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_{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 CO₂ flush in the drought plots after the end of the drought treatment (Fig. 2c).

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_{Soil} (Kim et al., 1992; Sowerby et al., 2008), while for mesic and drier habitats reduced F_{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 treatment itself, we also observed a significant reduction of cumulated F_{Soil} over the entire CO₂ measurement period by 22% during 250 d (Tables 3 and 5). Harper et al. (2005) suggested that drought affects F_{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_{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 approximately 30% (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_{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 forests soils primarily reduced the respiration losses of radiocarbon-old CO₂.

Drought reduced the litter-derived soil CO₂ efflux (F_{Litter}) significantly for the drought period (69 d; Fig. 2c, Table 4). The peak of F_{Litter} after rewetting was, however, less pronounced than the observed value for total soil CO₂ efflux (Figs. 1 and 3), possibly

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because the real CO₂ flush from the litter was missed by the weekly measurements. Despite increasing F_{Litter} after the drought, drought decreased the total litter-derived CO₂ efflux and the ratio of $F_{\text{Litter}}/F_{\text{Soil}}$ for the entire ¹³C measurement period (Table 4), which is in agreement with the observations of Xu and Baldocchi (2004) and Chou et al. (2008) in Mediterranean grasslands. However, it is not clear, if the measurement period in our study was long enough to capture the full effect of the drought on the microbial activity. Hence, it is possible that the temporarily reduced F_{Soil} might get compensated later through a delayed decomposition of labile components and/or a retarded priming (Subke et al., 2006). The apparent compensation of the suppressed F_{Litter} under drought by an increased mineralization after rewetting (Table 4) possibly does not occur under farming conditions due to the ongoing litter supply. However, drought also reduces plant productivity and thus, the litter input into soils.

4.4 Relationships of soil CO₂ efflux and its sources to environmental factors

Soil temperature (T_S) and soil moisture (Θ_V) are the most important factors controlling soil CO₂ efflux (F_{Soil}) on local and global scales (e.g. Pavelka et al., 2007; Raich and Schlesinger, 1992). In a recent compilation of soil respiration studies in European grasslands, Bahn et al. (2008) found mean annual T_S to be a very good predictor of annual F_{Soil} under natural litterfall conditions across sites. Our results from the control plots confirm these observations, 42% of the variance in our observed F_{Soil} were explained by T_S at 5 cm depth over the entire CO₂ measurement period. Our estimated Q_{10} of 3.3 lies well within the range for 20 grasslands across Europe given by Bahn et al. (2008). The relationship between F_{Soil} and Θ_V showed greater scatter than between F_{Soil} and T_S similar to results reported previously (e.g. Knapp et al., 1998). Θ_V at 5 cm depth was not significantly related to F_{Soil} (Table 2). One possible explanation could be the reliability of Θ_V measurements especially during the dry summertime. Another reason could be that microbial activity at the soil surface or in the litter was enhanced even by very short rainfall events especially in dry soils (Austin et al., 2004), thus, litter decomposition and F_{Soil} at the surface probably responded more rapidly to rainfall than

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soil moisture at 5 cm depth. However, most of the variation in F_{Soil} was explained when taking both environmental factors, Θ_V and T_S , into consideration (Table 2).

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. Furthermore, 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 CO_2 release. Despite a CO_2 flush at rewetting – the so-called “Birch-effect” – the reduction in F_{Soil} during drought was not fully compensated over the entire ^{13}C measurement period (179 d). Thus, our findings indicate that drought decreased C losses from soil for one growing season. If this holds true over several years and belowground plant productivity would remain largely unaffected by drought, these grassland soils could accumulate additional C under a drier climate. However, the long-term response might additionally depend on the acclimation of soil CO_2 efflux and plant productivity to prolonged and repeated drought.

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Table 1. Soil properties of topsoil 0–10 cm (means±standard errors; $n=2$ and 41 are shown in brackets; Roth, 2007).

Soil type ¹	Cambisol
Sand (g kg ⁻¹) ²	306±52 (2)
Silt (g kg ⁻¹) ³	477±25 (2)
Clay (g kg ⁻¹) ⁴	217±27 (2)
Bulk density (g cm ⁻³)	1.1±0.0 (41)
pH value	5.3±0.0 (2)
C _{org} (g kg ⁻¹)	31.0±0.8 (41)
N _{total} (g kg ⁻¹)	3.4±0.1 (41)
C/N	9.4±0.1 (41)
C _{org} stock (t ha ⁻¹)	32.9±2.2 (41)

¹ Classified after WRB Classification (FAO, 2006).

² <2000–63 μm.

³ <63–2 μm.

⁴ <2 μm.

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Table 2. Relationships between soil-, litter- and belowground-derived CO₂ efflux (F_{Soil} , F_{Litter} and F_{BG} , respectively) and the main factors soil temperature (T_S) and soil moisture (Θ_V) for drought and control plots combined (Drought+Control), for control (Control) and drought plots (Drought). The entire CO₂ measurement period lasted 250 d (DOY 92–342) with 25 measurement dates for F_{Soil} . The flux partitioning into F_{Litter} and F_{BG} was conducted for 179 d (DOY 117–295; $n=12$). The drought period in 2007 lasted from DOY 122 until DOY 191 (69 d; $n=5$ for all fluxes). Best fits are indicated with bold letters.

	Period	Factor	Adjusted R^2		
			Drought+Control	Control	Drought
F_{Soil}	CO ₂ measurement period	T_S	0.45***	0.42***	0.45***
		Θ_V	0.00	0.01	-0.03
		$T_S+\Theta_V$	0.50***	0.44***	0.56***
Drought period		T_S	0.25*	-0.10	0.19
		Θ_V	0.68**	0.75**	-0.30
		$T_S+\Theta_V$	0.60**	0.15	0.21
F_{Litter}	¹³ C measurement period	T_S	-0.04	-0.06	-0.03
		Θ_V	-0.01	-0.01	0.33**
		$T_S+\Theta_V$	-0.02	-0.07	0.03
Drought period		T_S	-0.04	-0.29	-0.31
		Θ_V	0.45**	-0.09	-0.20
		$T_S+\Theta_V$	0.11	-0.32	-0.31
F_{BG}	¹³ C measurement period	T_S	0.35***	0.34**	0.43**
		Θ_V	0.27**	0.66***	0.06
		$T_S+\Theta_V$	0.60***	0.69***	0.66***
Drought period		T_S	0.17	0.01	0.56*
		Θ_V	0.81***	-0.36	0.29
		$T_S+\Theta_V$	0.85***	0.19	0.57*

Formulas: $T_S = a \cdot \exp(b \cdot T_S)$

$\Theta_V = a \cdot \theta_V^2 + d \cdot \theta_V - f$

$T_S + \Theta_V = a \cdot \exp(b \cdot T_S) \cdot (c \cdot \theta_V^2 + d \cdot \theta_V - f)$

Significance codes: $P < 0.001$ ***; $0.001 < P < 0.05$ **; $0.05 < P < 0.1$ *.

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Table 3. Effects of drought on cumulated soil CO₂ effluxes for the for the drought period (69 d), the CO₂ measurement period (250 d) and the whole year 2007. Diff. (%): percentage change due to drought (Diff.=(Drought–Control)/Control*100).

	Control (g C m ⁻²)	Drought (g C m ⁻²)	Diff. (%)
Drought period	717	343	-52
CO ₂ measurement period	1497	1166	-22
Annual flux	1696	1366	-19

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Table 4. Effects of drought on grassland soil CO₂ 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_{Soil} , $F_{\text{Litter}}/F_{\text{Soil}}$, F_{Litter} and F_{BG} are shown for the the drought period (69 d) and the entire ¹³C measurement period (179d) in 2007. Diff. (%): percentage difference between control and drought (Diff.=(Drought–Control)/Control*100).

		Drought period (DOY 122–191)			¹³ C measurement period (DOY 117–295)		
		Control	Drought	Diff. (%)	Control	Drought	Diff. (%)
F_{Soil}	(g C m ⁻²)	716	343	–52***	1428	975	–32***
F_{Litter}	(g C m ⁻²)	216	56	–74***	267	180	–33***
$F_{\text{Litter}}/F_{\text{Soil}}$	(%)	30	16	–46**	19	18	–1.2
F_{BG}	(g C m ⁻²)	500	288	–43***	1025	795	–22***

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

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Table 5. Statistical significance of F_{Soil} , F_{Litter} , $F_{\text{Litter}}/F_{\text{Soil}}$, F_{BG} and $F_{\text{BG}}/F_{\text{Soil}}$ during the drought period (69 d) and the entire ¹³C measurement period (179 d) in 2007. Degrees of freedom (df), F - and P -values from two-way ANOVA are shown (factors: sampling date and drought treatment).

		Drought period (DOY 122–191)			¹³ C measurement period (DOY 117–295)		
		df	F	P	df	F	P
F_{Soil}	Sampling date	4	1.68	0.19	12	10.06	<0.001
	Drought treatment	1	87.94	<0.001	1	77.62	<0.001
	Interaction	4	5.46	0.003	12	12.61	<0.001
F_{Litter}	Sampling date	4	35.27	<0.001	12	20.28	<0.001
	Drought treatment	1	115.89	<0.001	1	24.54	<0.001
	Interaction	4	35.25	<0.001	12	23.39	<0.001
$F_{\text{Litter}}/F_{\text{Soil}}$	Sampling date	4	7.64	<0.001	12	9.03	<0.001
	Drought treatment	1	8.34	0.009	1	0.47	0.49
	Interaction	4	2.85	0.05	12	3.75	<0.001
F_{BG}	Sampling date	4	1.64	0.20	12	6.96	<0.001
	Drought treatment	1	29.78	<0.001	1	46.40	<0.001
	Interaction	4	0.38	0.81	12	2.97	0.003
$F_{\text{BG}}/F_{\text{Soil}}$	Sampling date	4	7.64	<0.001	12	9.03	<0.001
	Drought treatment	1	8.34	0.009	1	0.47	0.49
	Interaction	4	2.85	0.05	12	3.75	<0.001

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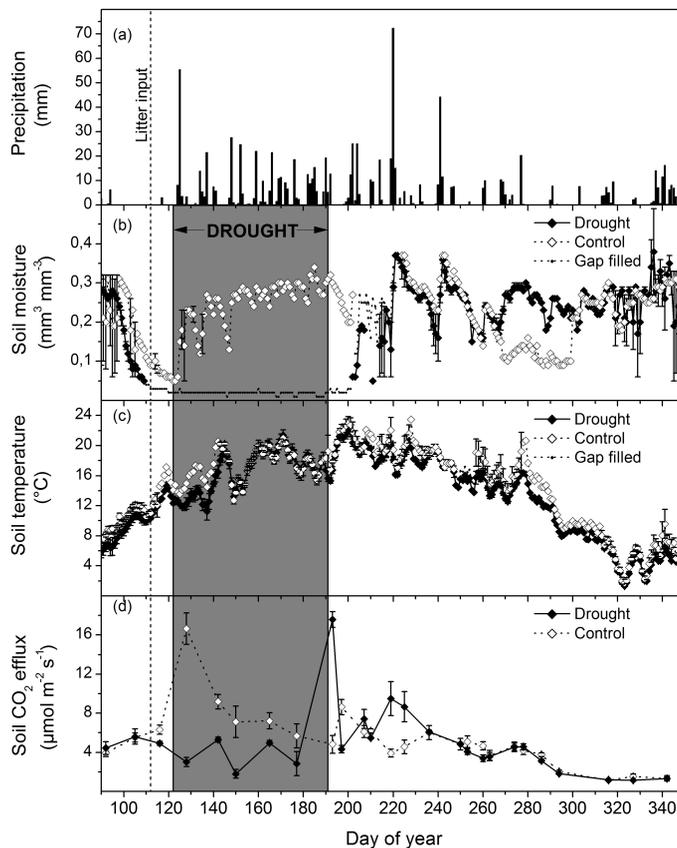


Fig. 1. Precipitation, soil climate and soil CO₂ efflux measured in drought and control plots during a litter addition experiment in 2007. **(a)** Daily ambient precipitation from adjacent meteorological station (Zeeman et al., 2009). **(b)** Daily soil moisture at 5 cm depth. **(c)** Daily soil temperature at 5 cm depth. **(d)** Soil CO₂ efflux measured biweekly. Means and standard errors for CO₂ $n=3$, for soil temperature and moisture $n=2$.

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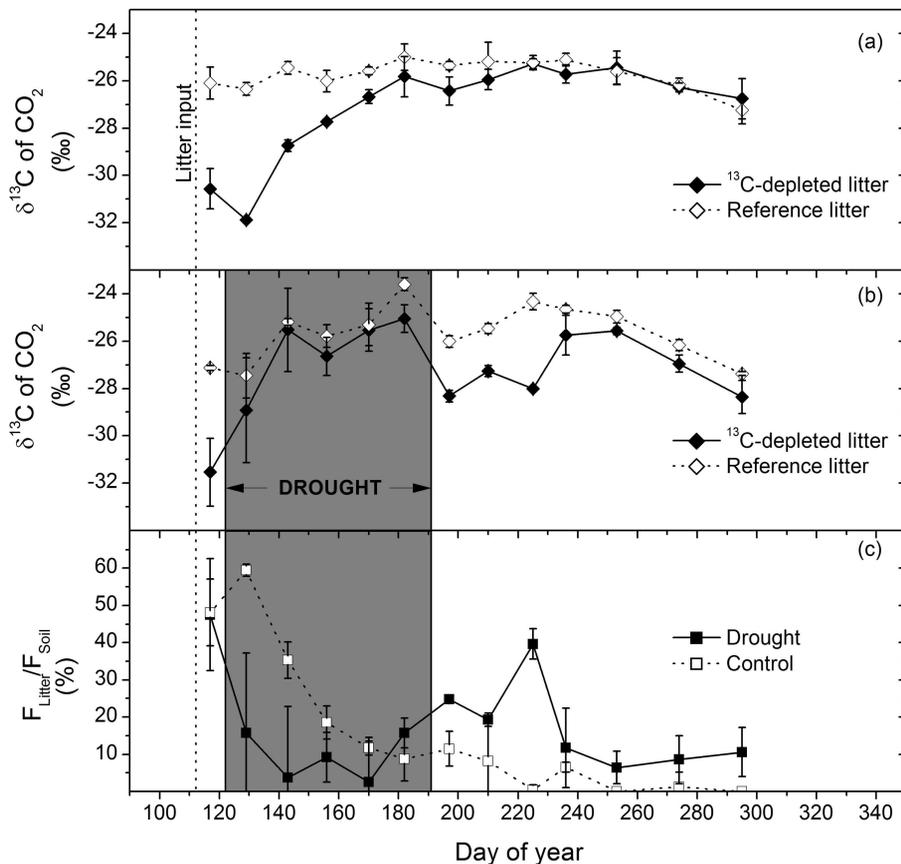


Fig. 2. $\delta^{13}\text{C}$ values of soil CO₂ efflux for control plots (a) and for drought plots (b) from ^{13}C -depleted and reference litter during the entire ^{13}C measurement period as well as proportion of litter-derived CO₂ from the total soil CO₂ efflux in per cent for drought and control plots during the entire ^{13}C measurement period (c). Means and standard errors of three plots per treatment.

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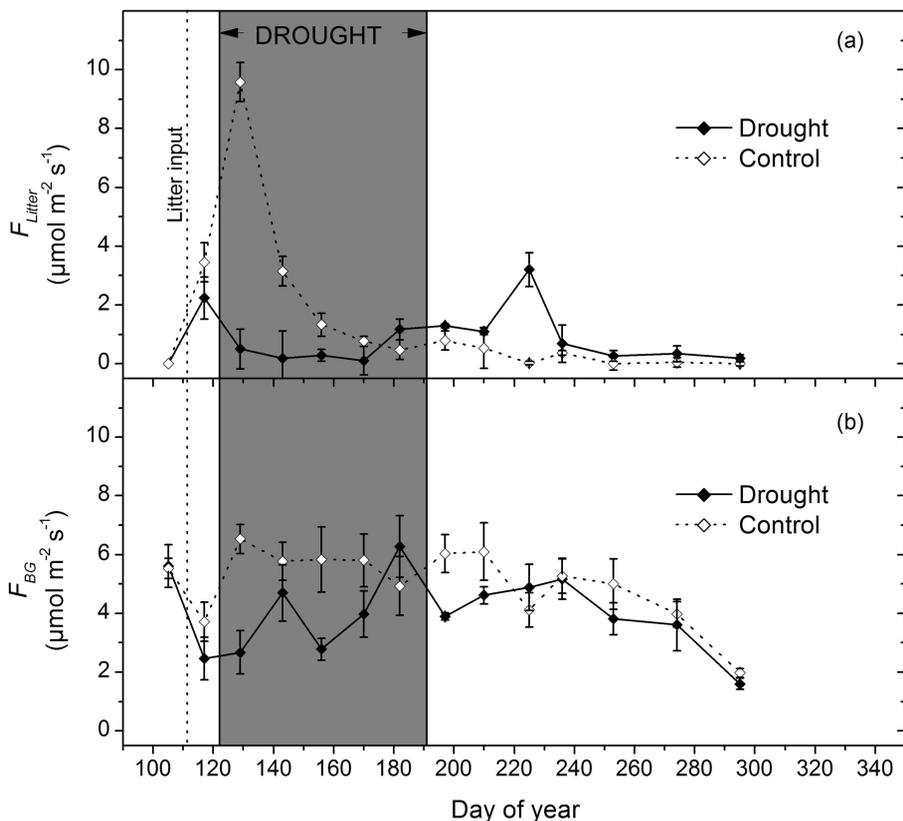


Fig. 3. (a) Litter-derived (F_{Litter}) and (b) belowground-derived CO₂ efflux (F_{BG}) during the entire ¹³C measurement period in 2007. Means and standard errors of three plots per treatment.

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