Biogeosciences

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_{Soil}) and on the contribution of litter to F_{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_{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_{Soil} in our litter addition experiment by 59% and F_{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_{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_{Soil} and F_{Litter} during the entire ^{13}C measurement period (April to October) by 26% and 37%, respectively. Overall, our findings show that drought decreased F_{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.

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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_{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_{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; 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 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 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_{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., 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 (Borken et al., 2006; Inglima 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 (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_{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 rain shelters to simulate a summer drought in a temperate grassland and separated the litter- and belowground-derived components 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 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_{Soil}) were conducted in a core area (1 m×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 ECH$_2$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 CO$_2$ efflux measurement

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 ^{13}C-depleted ($-37.2\pm0.1‰$ (V-PDB)) or reference litter ($-27.9\pm0.1‰$ (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 CO$_2$ 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 CO$_2$ 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 CO$_2$ efflux was measured using a soil CO$_2$ 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 cm^3). In total, we performed 26 CO$_2$ 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 CO$_2$ and calculation of litter-derived CO$_2$

To estimate the δ^{13}C of soil respired CO$_2$, 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 CO$_2$ 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 δ^{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

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.

to an automated online purification and pre-concentration system (Gasbench II; ThermoFinnigan MAT, Bremen, Germany), which was linked to an isotope ratio mass spectrometer (Delta^{Plus} XL, ThermoFinnigan MAT) for the determination of δ^{13}C. The δ^{13}C values of CO$_2$ 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 CO$_2$ and atmospheric CO$_2$. To estimate the δ^{13}C values of the respired CO$_2$, we applied the so-called Keeling plot approach (Pataki et al., 2003) by regressing δ^{13}C versus 1/CO$_2$ concentration. The resulting y-intercept represents the δ^{13}C of the respiratory CO$_2$ 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 CO$_2$ efflux we estimated the δ^{13}C of the respired CO$_2$ of subplots with ^{13}C-depleted and reference litter. We calculated the contribution of fresh litter to soil CO$_2$ efflux (F_{Litter}/F_{Soil}) by a single isotope linear mixing model based on mass conservation equations (Balesdent et al., 1987):

$$F_{Soil} = F_{Litter} + F_{BG}, \tag{1}$$

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

where F_{Soil} is the total soil CO$_2$ efflux and δ is the isotopic composition of soil CO$_2$ estimated with Keeling plots. The mixing model is based on the two end-members, δ_{Litter} (isotopic composition of litter-respired CO$_2$) and δ_{BG} (isotopic composition of belowground CO$_2$ including CO$_2$ 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 ^{13}C-depleted litter; Ngao et al., 2005). We estimated δ_{BG} by applying Eq. (2) for both ^{13}C-litter treatments, assuming that there are no priming effects and thus no differences of F_{Litter}/F_{Soil} between both treatments:

$$F_{Litter}/F_{Soil} = (\delta_D - \delta_{BGD})/(\delta_{LitterD} - \delta_{BGD})$$
$$= (\delta_R - \delta_{BGR})/(\delta_{LitterR} - \delta_{BGR}). \quad (3)$$

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:

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

We estimated the isotopic compositions of respired CO_2 (δ_R and δ_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_{Litter}/F_{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_{Soil}), litter- (F_{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_{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. The temperature dependency of soil CO_2 effluxes was estimated by fitting measured fluxes to the function of Lloyd and Taylor (1994):

$$F_{Soil} = a \cdot \exp^{(b*Ts)}, \quad (5)$$

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 θ_V at 30 cm depth, we used negative quadratic functions according to Mielnick and Dugas (2000):

$$F_{Soil} = c \cdot \theta_V^2 + d*\theta_V - f, \quad (6)$$

with c, d, and f as fitted constants.

Furthermore, we assessed interactive effects of T_S at 5 cm and θ_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 (θ_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_{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_{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_{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 (θ_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 δ^{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 (θ_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
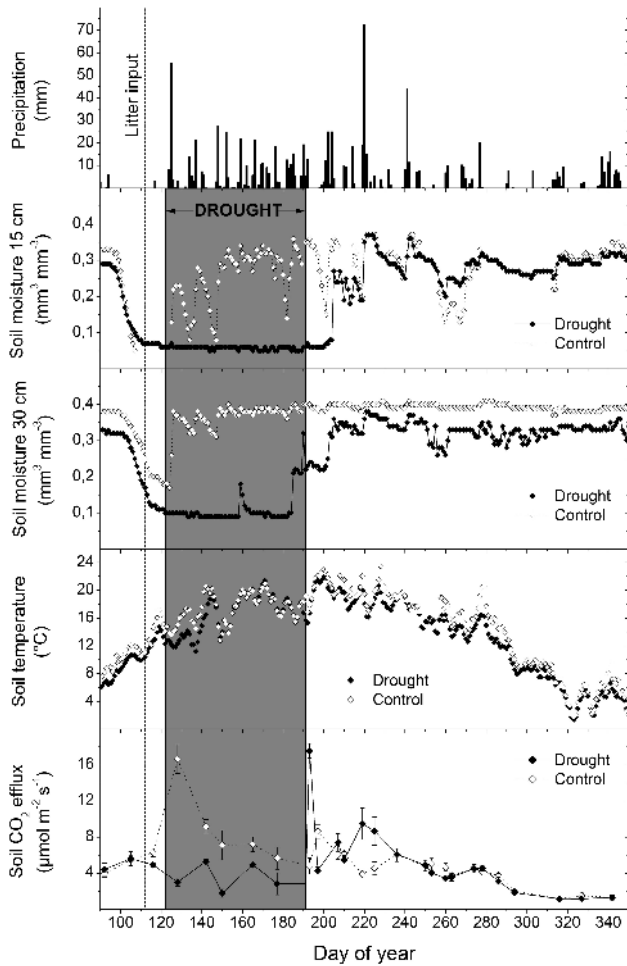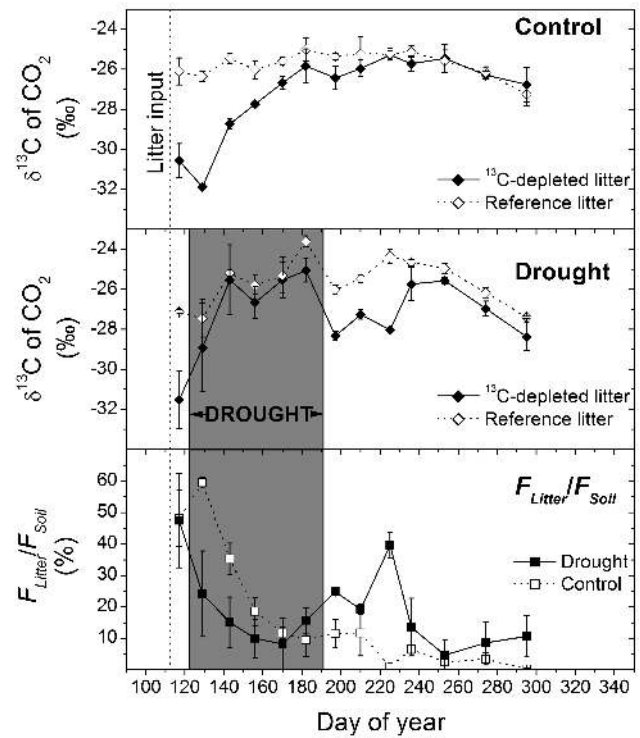
Fig. 1. Precipitation, soil moisture at 15 and 30 cm depth, soil temperature at 5 cm depth and soil CO_2 efflux measured in drought and control plots during a litter addition experiment in 2007. Means and standard errors for soil CO_2 effluxes of three plots.

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_{Litter} and F_{BG}) during a litter addition experiment in 2007. Means and standard errors of three plots.

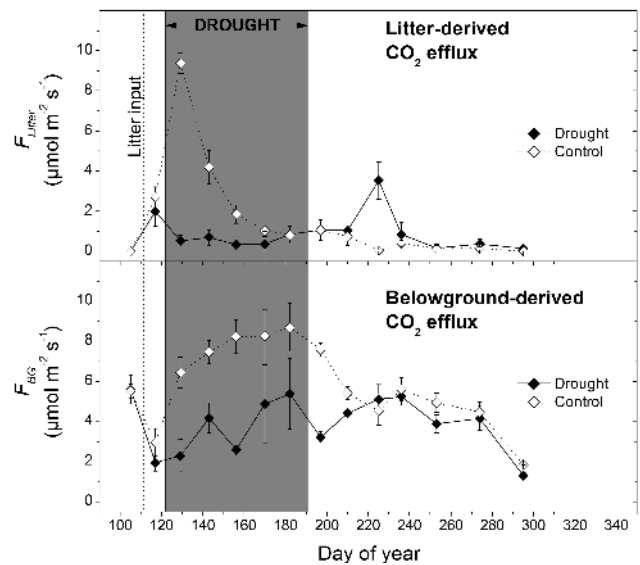to determine the temperature sensitivity. The combination of T_S and θ_V improved the regression model significantly (R^2=0.84, $P < 0.001$, n=12; Table 2). Between April and October 2007 the cumulative sums of F_{Soil} and F_{Litter} in the control plots were 1.29 kg C m^{-2} and 0.27 kg C m^{-2} respectively, yielding an average F_{Litter}/F_{Soil} of around 21%. The total F_{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_{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_{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_{Soil} and soil moisture (θ_V) at any depth

Table 2. Relationships of soil-, litter- and belowground-derived CO_2 effluxes (F_{Soil}, F_{Litter} and F_{BG}, respectively) to soil temperature at 5 cm (T_S) and soil moisture at 30 cm depth (θ_V) (regression coefficients and temperature sensitivity coefficient ($Q_{10}=e^{10 \cdot b}$)). The CO_2 measurement period data was only used between DOY 116–294 with 20 measurement dates for F_{Soil}. The measurements of F_{Litter} and F_{BG} were conducted for 179 days (DOY 117–295; $n=12$). Best fits are indicated with bold letters.

	Factor	Adjusted R^2			Q_{10}	
		Total	Control	Drought	Control	Drought
F_{Soil}	T_S	0.46***	0.44***	0.45***	1.83	2.13
	θ_V	n.s.	n.s.	n.s.		
	$T_S+\theta_V$	**0.52***	**0.67***	**0.59***		
F_{Litter}	T_S	n.s.	n.s.	n.s.	n.d.	n.d.
	θ_V	n.s.	0.70***	**0.17***		
	$T_S+\theta_V$	**0.12***	**0.84***	**0.27***		
F_{BG}	T_S	0.40***	0.40**	0.46**	2.16	1.97
	θ_V	0.21**	0.39**	n.s.		
	$T_S+\theta_V$	**0.56***	**0.70***	**0.65***		

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: $P < 0.001$***; $0.001 < P < 0.05$**; $0.05 < P < 0.1$*; $P > 0.1$=n.s.
n.d.=not determinable.

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

The litter-derived CO_2 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 (Fig. 3). The contribution of fresh litter to total soil CO_2 efflux (F_{Litter}/F_{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 sensitively to drought than total F_{Soil}. The ratio of F_{Litter}/F_{Soil} started to rise again after the drought and reached a second peak value of 40% in August (Fig. 2). Subsequently, F_{Litter}/F_{Soil} declined and remained on a level of around 10% until the end of the experiment. The average F_{Litter}/F_{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 CO_2 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 CO_2 efflux by $0.09 \, kg \, C \, m^{-2}$, which corresponds to a 37% decrease compared to the control ($P=0.33$). Under drought, F_{Litter} was less closely related to soil moisture than under ambient conditions (Table 2).

4 Discussion

4.1 Soil CO_2 efflux

The seasonal pattern of soil CO_2 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_{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_{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_{Soil} (Table 2) although the temperature dependency was superimposed by the litter addition.

The estimated mean annual soil CO_2 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_{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_{Soil}, F_{Litter}/F_{Soil}, F_{Litter} and F_{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·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})	620	257	−59**	1198	889	−26**
F_{Litter}	(g C m^{-2})	206	40	−81**	260	164	−37
F_{Litter}/F_{Soil}	(%)	30	16	−46	21	18	−11
F_{BG}	(g C m^{-2})	414	217	−48***	938	725	−23**

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

Table 4. Statistical significance of F_{Soil}, F_{Litter}, F_{Litter}/F_{Soil}, F_{BG} and F_{BG}/F_{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).

		Drought period (DOY 122–191)			^{13}C measurement period (DOY 117–295)		
		df	F	P	df	F	P
F_{Soil}	Sampling date	4	1.7	0.19	12	10.6	< 0.001
	Drought treatment	1	16.8	< 0.05	1	6.2	< 0.05
	Interaction	4	5.5	0.003	12	12.6	< 0.001
F_{Litter}	Sampling date	4	2.8	0.05	12	20.3	< 0.001
	Drought treatment	1	16.6	< 0.05	1	1.1	0.33
	Interaction	4	0.8	0.57	12	23.4	< 0.001
F_{Litter}/F_{Soil}	Sampling date	4	7.6	< 0.001	12	9.0	< 0.001
(F_{BG}/F_{Soil})	Drought treatment	1	2.9	0.16	1	0.13	0.72
	Interaction	4	2.9	0.05	12	3.8	< 0.001
F_{BG}	Sampling date	4	1.6	0.20	12	7.0	< 0.001
	Drought treatment	1	78.0	< 0.001	1	15.6	0.002
	Interaction	4	0.4	0.81	12	3.0	0.003

added litter (0.35 kg C m^{-2} corresponding to 165% of annual litterfall), because we did not apply farmyard manure (normally: 0.4 kg C m^{-2}yr^{-1} in 2007; Zeeman et al., 2009) and we prevented natural litterfall in our plots. Thus, the total annual C input 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 on fertile soils driven by high summer soil temperatures combined with almost optimal soil moisture.

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_{Litter}/F_{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_{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_{Litter}) declined exponentially from April to October and amounted to approximately 0.27 kg C m^{-2}, corresponding to 21% of F_{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_{Soil} (mean value of 25 temperate grassland studies reviewed by Wang and Fang, 2009), F_{Litter} would correspond to about 25% of the heterotrophic part of F_{Soil}.

Our results show that the two components of F_{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_{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_{Litter} to drought than of F_{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_{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 con-

trasts 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_{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 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. 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_{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_{Soil} (Kim et al., 1992; Davidson et al., 2004; 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 period itself, we also observed a significant reduction of cumulated F_{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_{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 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_{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_{Litter}) significantly for the drought period (69 days; Fig. 2, Table 3). The peak of F_{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_{Litter} after the drought, drought decreased the total litter-derived CO_2 efflux and the ratio of F_{Litter}/F_{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_{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_{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.

References

Amundson, R.: The carbon budget in soils, Annu. Rev. Earth Planet. Sci., 29, 535–562, 2001.

Bahn, M., Rodeghiero, M., Anderson-Dunn, M., Dore, S., Gimeno, C., Drosler, M., Williams, M., Ammann, C., Berninger, F., Flechard, C., Jones, S., Balzarolo, M., Kumar, S., Newesely, C., Priwitzer, T., Raschi, A., Siegwolf, R., Susiluoto, S., Tenhunen, J., Wohlfahrt, G., and Cernusca, A.: Soil respiration in European grasslands in relation to climate and assimilate supply, Ecosystems, 11, 1352–1367, 2008.

Balesdent, J., Mariotti, A., and Guillet, B.: Natural ^{13}C abundance as a tracer for studies of soil organic-matter dynamics, Soil Biol. Biochem., 19, 25–30, 1987.

Barnard, R., Le Roux, X., Hungate, B. A., Cleland, E. E., Blankinship, J. C., Barthes, L., and Leadley, P. W.: Several components of global change alter nitrifying and denitrifying activities in an annual grassland, Funct. Ecol., 20, 557–564, 2006.

Bessler, H., Temperton, V. M., Roscher, C., Buchmann, N., Schmid, B., Schulze, E. D., Weisser, W. W., and Engels, C.: Aboveground overyielding in grassland mixtures is associated with reduced biomass partitioning to belowground organs, Ecology, 90, 1520–1530, 2009.

Birch, H. F.: Pattern of humus decomposition in East African soils, Nature, 181, 788–788, 1958.

Borken, W., Savage, K., Davidson, E. A., and Trumbore, S. E.: Effects of experimental drought on soil respiration and radiocarbon efflux from a temperate forest soil, Glob. Change Biol., 12, 177–193, 2006.

Borken, W. and Matzner, E.: Reappraisal of drying and wetting effects on C and N mineralization, Glob. Change Biol., 15, 808–824, 2009.

Bowden, R. D., Nadelhoffer, K. J., Boone, R. D., Melillo, J. M., and Garrison, J. B.: Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperature mixed hardwood forest, Can. J. For. Res.-Rev. Can. Rech. For., 23, 1402–1407, 1993.

Bremer, D. J., Ham, J. M., Owensby, C. E., and Knapp, A. K.: Responses of soil respiration to clipping and grazing in a tallgrass prairie, J. Environ. Qual., 27, 1539–1548, 1998.

Buyanovsky, G. A., Kucera, C. L., and Wagner, G. H.: Comparative analysis of carbon dynamics in native and cultivated ecosystems, Ecology, 68, 2023–2031, 1987.

Chou, W. W., Silver, W. L., Jackson, R. D., Thompson, A. W., and Allen-Diaz, B.: The sensitivity of annual grassland carbon cycling to the quantity and timing of rainfall, Glob. Change Biol., 14, 1382–1394, 2008.

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A. D., Friedlingstein, P.,

Grünwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J. F., Sanz, M. J., Schulze, E.D., Vesala, T., and Valentini, R.: Europe-wide reduction in primary productivity caused by the heat and drought in 2003, Nature, 437, 529–533, 2005.

Davidson, E., Ishida, F. Y., and Nepstad, D. C.: Effects of an experimental drought on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest, Glob. Change Biol., 10, 718–730, 2004.

Denef, K., Six, J., Paustian, K., and Merckx, R.: Importance of macroaggregate dynamics in controlling soil carbon stabilization: short-term effects of physical disturbance induced by dry-wet cycles, Soil Biol. Biochem., 33, 2145–2153, 2001.

FAO: World reference base of soil resources 2006, A framework for international classification, correlation and communication, Food and Agriculture Organisation, Rome, Italy, 1–128, 2006.

Fierer, N. and Schimel, J. P.: A proposed mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil, Soil Sci. Soc. Am. J., 67, 798–805, 2003.

Freeman, C., Liska, G., Ostle, N. J., Lock, M. A., Reynolds, B., and Hudson, J.: Microbial activity and enzymic decomposition processes following peatland water table drawdown, Plant Soil, 180, 121–127, 1996.

Flechard, C. R., Neftel, A., Jocher, M., Ammann, C., Leifeld, J., and Fuhrer, J.: Temporal changes in soil pore space CO2 concentration under permanent grassland, Agr. Forest Meteorol., 142, 66–84, 2007.

Garten, C. T., Classen, A. T., and Norby, R. J.: Soil moisture surpasses elevated CO$_2$ and temperature as a control on soil carbon dynamics in a multi-factor climate change experiment, Plant Soil, 319, 85–94, 2009.

Gilgen, A. K. and Buchmann, N.: Response of temperate grasslands at different altitudes to simulated summer drought differed but scaled with annual precipitation, Biogeosciences, 6, 2525–2539, 2009,
http://www.biogeosciences.net/6/2525/2009/.

Halverson, L. J., Jones, T. M., and Firestone, M. K.: Release of intracellular solutes by four soil bacteria exposed to dilution stress, Soil Sci. Soc. Am. J., 64, 1630–1637, 2000.

Harper, C. W., Blair, J. M., Fay, P. A., Knapp, A. K., and Carlisle, J. D.: Increased rainfall variability and reduced rainfall amount decreases soil CO$_2$ flux in a grassland ecosystem, Glob. Change Biol., 11, 322–334, 2005.

Hebeisen, T., Lüscher, A., and Nösberger, J.: Effects of elevated atmospheric CO$_2$ and nitrogen fertilisation on yield of Trifolium repens and Lolium perenne, Acta Oecol.-Int. J. Ecol., 18, 277–284, 1997.

Inglima, I., Alberti, G., Bertolini, T., Vaccari, F. P., Gioli, B., Miglietta, F., Cotrufo, M. F., and Peressotti, A.: Precipitation pulses enhance respiration of Mediterranean ecosystems: the balance between organic and inorganic components of increased soil CO$_2$ efflux, Glob. Change Biol., 15, 1289–1301, 2009.

Jackson, R. B., Canadell, J. Ehleringer, J. R., Mooney, H. A., Sala, O. E., and Schulze, E.-D.: A global analysis of root distributions for terrestrial biomes, Oecologia, 108, 389–411, 1996.

Johnson, L. C. and Matchett, J. R.: Fire and grazing regulate belowground processes in tallgrass prairie, Ecology, 82, 3377–3389,

2001.

Joos, O., Saurer, M., Heim, A., Hagedorn, F., Schmidt, M. W. I., and Siegwolf, R. T. W.: Can we use the CO$_2$ concentrations determined by continuous-flow isotope ratio mass spectrometry from small samples for the Keeling plot approach? Rapid Commun. Mass Sp., 22, 4029–4034, 2008.

Keeling, C. D.: The concentration and isotopic abundances of atmospheric carbon dioxide in rural areas, Geochim. Cosmochim. Ac., 13, 322–334, 1958.

Kim, J., Verma, S. B., and Clement, R. J.: Carbon-dioxide budget in a temperate grassland ecosystem, J. Geophys. Res.-Atmos., 97, 6057–6063, 1992.

Knapp, A. K. and Smith, M. D.: Interannual variability in net primary production and precipitation – Response, Science, 293, p. 1723a, 2001.

Knapp, A. K., Fay, P. A., Blair, J. M., Collins, S. L., Smith, M. D., Carlisle, J. D., Harper, C. W., Danner, B. T., Lett, M. S., and McCarron, J. K.: Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland, Science, 298, 2202–2205, 2002.

Lal, R.: Soil carbon sequestration to mitigate climate change, Geoderma, 123, 1–22, 2004.

Lloyd, J. and Taylor, J. A.: On the temperature-dependence of soil respiration, Funct. Ecol., 8, 315–323, 1994.

Luo, Y. Q., Hui, D. F., and Zhang, D. Q.: Elevated CO$_2$ stimulates net accumulations of carbon and nitrogen in land ecosystems: A meta-analysis, Ecology, 87, 53–63, 2006.

Luo, Y. Q.: Terrestrial carbon-cycle feedback to climate warming, Annu. Rev. Ecol. Evol. Syst., 38, 683–712, 2007.

Maier, C. A. and Kress, L. W.: Soil CO$_2$ evolution and root respiration in 11 year-old loblolly pine (Pinus taeda) plantations as affected by moisture and nutrient availability, Can. J. For. Res.-Rev. Can. Rech. For., 30, 347–359, 2000.

Meehl, G. A., Stocker, T. F., Collins, W. D., Friedlingstein, P., Gaye, A. T., Gregory, J. M., Kitoh, A., Knutti, R., Murphy, J. M., Noda, A., Raper, S. C. B., Watterson, I. G., Weaver, A. J., and Zhao, Z.-C.: Global climate projections, in: Climate change 2007: The physical science basis. contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change, edited by: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., and Miller, H. L., Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 2007.

Mielnick, P. C. and Dugas, W. A.: Soil CO$_2$ flux in a tallgrass prairie, Soil Biol. Biochem., 32, 221–228, 2000.

Muhr, J., Goldberg, S. D., Borken, W., and Gebauer, G.: Repeated drying/rewetting cycles and their effects on the emission of CO$_2$, N$_2$O, NO and CH$_4$ in a forest soil, J. Plant Nutr. Soil Sc., 171, 719–728, 2008.

Ngao, J., Epron, D., Brechet, C., and Granier, A.: Estimating the contribution of leaf litter decomposition to soil CO$_2$ efflux in a beech forest using ^{13}C-depleted litter, Glob. Change Biol., 11, 1768–1776, 2005.

Pataki, D. E., Ehleringer, J. R., Flanagan, L. B., Yakir, D., Bowling, D. R., Still, C. J., Buchmann, N., Kaplan, J. O., and Berry, J. A.: The application and interpretation of Keeling plots in terrestrial carbon cycle research, Global Biogeochem. Cy., 17, 1022, doi:10.1029/2001GB001850, 2003.

R Development Core Team: R: A language and environment for

statistical computing, R Foundation for statistical computing, Vienna, Austria, 2005.

Raich, J. W. and Schlesinger, W. H.: The global carbon-dioxide flux in soil respiration and its relationship to vegetation and climate, Tellus B, 44, 81–99, 1992.

Raich, J. W. and Tufekcioglu, A.: Vegetation and soil respiration: Correlations and controls, Biogeochemistry, 48, 71–90, 2000.

Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J., Valentini, R., Banza, J., Casals, P., Cheng, Y., Grünzweig, J.M., Irvine, J., Joffre, R., Law, B.E., Loustau, D., Miglietta, F., Oechel, W., Ourcival, J.-M., Pereira, J. S., Peressotti, A., Ponti, F., Qi, Y., Rambal, S., Rayment, M., Romanya, J. Rossi, F., Tedeschi, V., Tirone, G., Xu, M., and Yakir, D.: Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices, Global Biogeochem. Cy., 17, 15.1–15.15, 2003.

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

Roth, K.: Bodenkartierung und GIS-basierte Kohlenstoffinventur von Graslandböden, Diploma thesis, University of Zurich, Zurich, 1–115, 2007.

Ryan, M. G. and Law, B. E.: Interpreting, measuring, and modeling soil respiration, Biogeochemistry, 73, 3–27, 2005.

Scott, R. L., Jenerette, G. D., Potts, D. L., and Huxman, T. E.: Effects of seasonal drought on net carbon dioxide exchange from a woody-plant-encroached semiarid grassland, J. Geophys. Res., 114, G4004, doi:10.1029/2008JG000900, 2009.

Signarbieux, C.: Grasslands in a changing climate in Switzerland: photosynthetic performance and water relations of selected species under artificial drought, PhD Thesis, University of Bern, 127 pp., 2009.

Sowerby, A., Emmett, B. A., Tietema, A., and Beier, C.: Contrasting effects of repeated summer drought on soil carbon efflux in hydric and mesic heathland soils, Glob. Change Biol., 14, 2388–2404, 2008.

Subke, J. A., Inglima, I., and Cotrufo, M. F.: Trends and methodological impacts in soil CO$_2$ efflux partitioning: A metaanalytical review, Glob. Change Biol., 12, 921–943, 2006.

Theis, D. E., Jäggi, M., Äschlimann, D., Blum, H., Frossard, E., and Siegwolf, R. T. W.: Dynamics of soil organic matter turnover and soil respired CO$_2$ in a temperate grassland labelled with ^{13}C, Eur. J. Soil Sci., 58, 1364–1372, 2007.

Wan, S. and Luo, Y.: Substrate regulation of soil respiration in a tallgrass prairie; results of clipping and shading experiment, Global Biogeochem. Cy., 17, 1054, doi:10.1029/2002GB001971, 2003.

Wang, W. J., Dalal, R. C., Moody, P. W., and Smith, C. J.: Relationships of soil respiration to microbial biomass, substrate availability and clay content, Soil Biol. Biochem., 35, 273–284, 2003.

Wang, W. and Fang, J.: Soil respiration and human effects on global grasslands, Global Planet. Change, 67, 20–28, 2009.

White, A., Cannell, M. G. R., and Friend, A. D.: The high-latitude terrestrial carbon sink: a model analysis, Glob. Change Biol., 6, 227–245, 2000.

Zeeman, M. J., Tuzson, B., Emmenegger, L., Knohl, A., Buchmann, N., and Eugster, W.: Conditional CO$_2$ flux analysis of a managed grassland with the aid of stable isotopes, Biogeosciences Discuss., 6, 3481–3510, 2009,
http://www.biogeosciences-discuss.net/6/3481/2009/.