

Biogeochemistry (2014) 117:395–412
DOI 10.1007/s10533-013-9881-x

Experimental summer drought reduces soil CO₂ effluxes and DOC leaching in Swiss grassland soils along an elevational gradient

Frank Hagedorn · Ottmar Joos

Received: 8 March 2013 / Accepted: 11 June 2013 / Published online: 21 June 2013
© Springer Science+Business Media Dordrecht 2013

Abstract Soil moisture affects belowground activity in grasslands, but the effects of summer drought on different soil C fluxes is uncertain. Soil respiration (*SR*), dissolved organic carbon (DOC) leaching and their components may all respond differently and drought effects will interact with other factors such as temperature, making a priori predictions of soil C balances difficult. In this study, we used rain shelters to simulate summer droughts by reducing annual precipitation by around 30 % in three managed grassland sites at 400, 1,000 and 2,000 m a.s.l. in Switzerland covering a gradient in mean annual temperatures of 7.5 °C. During the growing season, we quantified the impacts of drought on *SR*, DOC leaching, litter decomposition and the contribution of ¹³C-depleted litter to DOC fluxes. Along the elevational gradient, *SR* rates did not decrease with increasing altitude. Thus, *SR* was higher at a given temperature at higher altitudes, which probably reflects more labile soil C and hence greater substrate availability in a colder climate. Fluxes of DOC at 5 cm

depth were a magnitude smaller than *SR* and did not show a pattern with elevation. At all altitudes, the experimental summer drought significantly reduced *SR* rates by 25–57 % and DOC leaching by 80–100 %, with a declining contribution of ¹³C-depleted litter-DOC. The remaining litter mass after drought was two to seven times larger as compared to the control. We did not observe a strong C release upon rewetting and hence, there was no compensation for the reduced soil C fluxes during drought. The more sensitive drought response in the litter layer than in the deeper soil and the declining DOC fluxes indicate an altered soil C balance with a C preservation in the topsoil, but ongoing losses of probably ‘older’ C in subsoils under drought.

Keywords Climate change · Drought · Soil moisture · Litter decomposition · Soil organic carbon · Soil respiration · Dissolved organic carbon · Temperature · Altitude

Introduction

Grasslands cover ~40 % of the ice-free global land surface (White et al. 2000) and comprise 30 % of European ecosystems (Arrouays et al. 2001). Grasslands constitute relatively large soil organic carbon stocks, because a large fraction of biomass is allocated belowground. Globally, grasslands store ~28–37 % of the terrestrial soil organic C pool and play a critical

Responsible Editor: Oliver van Straaten

F. Hagedorn (✉) · O. Joos
Swiss Federal Institute for Forest, Snow and Landscape
Research WSL, Birmensdorf, Switzerland
e-mail: hagedorn@wsl.ch; frank.hagedorn@wsl.ch

O. Joos
Department of Geography, University of Zurich, Zurich,
Switzerland

role in the carbon cycle (Lal 2004). Climate change scenarios of current climate models for Europe predict drier summers and reduced annual precipitation, and thus, more frequent summer droughts (Luterbacher et al. 2004; Meehl et al. 2007). This will affect terrestrial ecosystems as precipitation is among the primary controls on ecosystem processes e.g. net primary production (e.g. Ciais et al. 2005; Knapp and Smith 2001; Schwalm et al. 2012), litter decomposition (e.g. Kreyling et al. 2008; Risch et al. 2007), and soil respiration (*SR*) (e.g. Chou et al. 2008; Joos et al. 2010). The effects of extreme weather events on these processes are likely to be much stronger than the effects of changes in mean values of temperature and rainfall (Borken and Matzner 2009; Meehl et al. 2000). However, they have not yet received the deserved attention, and thus, general mechanisms of ecosystem responses to extreme weather events have not yet been fully identified (Jentsch 2006).

Soil CO₂ efflux (*SR*) is one of the largest C fluxes between ecosystems and the atmosphere (Raich and Schlesinger 1992). Global annual estimates suggest that around 58 Pg of CO₂-C is released from soils, in contrast to only 6 Pg from fossil fuel emissions and 2 Pg from land-use change (Houghton 2007). Due to the direct limitation of soil microbial activity and root activity by water availability, drought strongly affects *SR* (Manzoni et al. 2012; Schimel et al. 2007). The response differs, however, between autotrophic and heterotrophic respiration (Borken et al. 2006; Muhr and Borken 2009; Sanaullah et al. 2012), as well as between individual decomposer groups with microfauna and bacteria being more drought sensitive than fungi (Manzoni et al. 2012). Within a soil profile, litter decomposition might be more responsive than respiratory activity in the deeper soils because soils are more prone to drying at the surface (Joos et al. 2010). However, in Mediterranean ecosystems, Dirks et al. (2010) observed that high atmospheric water vapor provided enough moisture for the decomposition of significant amounts of litter even during the rainless summer season. Rewetting after drought was frequently found to induce a mineralization burst, the so-called ‘birch’ effect where the release of lysed microbial cells and the destabilization of organic matter by aggregate disruption and desorption of soil organic matter (SOM) lead to extraordinary high soil CO₂ effluxes (Borken and Matzner 2009; Schimel et al. 2007). If the rewetting pulse compensates for the

reduced C losses during the drought depends on a number of factors such as soil properties, vegetation type, intensity and length of the drying and rewetting (Manzoni et al. 2012; Muhr et al. 2010). All of these findings indicate that drought will strongly alter the sources of *SR* and the magnitude of drought responses will differ strongly among ecosystems and depend on the severity of droughts. This makes predictions of the soil C balance under a drier climate rather difficult.

Fluxes of dissolved organic carbon (DOC) are generally much smaller than *SR*, but DOC is a transient stage during SOM decomposition, and thus, the C flux associated with DOC turnover is an important component in terrestrial C cycling (Siemens 2003; Kindler et al. 2010). Moreover, the sorption of DOC in the mineral soil can contribute significantly to the long-term accumulation and preservation of organic C (Kaiser and Guggenberger 2000; Kaiser and Kalbitz 2012). In principal, DOC in soils results from microbial activity, root exudation or leaching from litter and humus, but the relative importance of these sources is still uncertain and differs among ecosystems and soil types (Hagedorn et al. 2004; Kalbitz et al. 2000; Sanderman and Amundson 2008). The fate of DOC within soils is strongly controlled by the transport with water and physico-chemical retention (e.g. Kaiser and Kalbitz 2012) and depends on soil characteristics, biological constraints and the contact time with the decomposer community (Don and Schulze 2008). In soils, drought suppresses DOC fluxes due to declining water fluxes, but promotes the DOC release upon rewetting (Hentschel et al. 2007). Field studies in forest soils, however, have failed to observe this flushing effect for DOC (Graf Pannatier et al. 2011).

In grasslands, the C cycle is particularly tightly coupled with the magnitude and timing of precipitation (Knapp and Smith 2001; Knapp et al. 2002) and precipitation is well established as a key determinant of biological activity (e.g. Lieth 1975; Harper et al. 2005; Weltzin et al. 2003). However, the majority of climate manipulation studies in grasslands have focused on responses of plant productivity to changes in precipitation amounts and patterns and much less attention has been paid to belowground C fluxes (e.g. De Boeck and Verbeeck 2011; Gilgen and Buchmann 2009). In comparison to forest ecosystems, there are only a few studies on DOC in grasslands although soil DOC fluxes are in the same magnitude in both ecosystem types (Don and Schulze 2008; Kindler

et al. 2010). To our knowledge, none of the studies have investigated the impacts of drought on DOC fluxes in grasslands.

In addition to soil moisture, temperature is a key environmental driver of soil C fluxes (e.g. Davidson and Janssens 2006). If and for how long climatic warming enhances *SR* is controversial as the stimulating effect by increased temperatures might be limited by a decreasing substrate availability and/or a thermal adaptation of plant and microbial communities (Conant et al. 2011; Eliasson et al. 2005). Moreover, there is a strong interaction between increasing temperature and soil moisture with a decreasing soil moisture restricting the stimulation of *SR* in warmer soils and with higher water losses in a warmer climate inducing a more rapid limitation by water (e.g. Schindlbacher et al. 2012). Because experimental temperature manipulations are associated with shortcomings, climatic gradients either along latitude or altitude provide alternative natural experimental set-ups to study warming effects on C dynamics in the long-term (e.g. Caprez et al. 2012; Zimmermann et al. 2009).

The aim of this study was to quantify soil C fluxes in grasslands along an elevational gradient and to assess the effects of a prolonged summer drought on *SR*, DOC fluxes and their litter-derived components in grasslands of Switzerland. We simulated predicted summer drought conditions in the field by installing rain shelters at three different altitudes (400, 1,000 and 2,000 m a.s.l.) and monitored the responses of *SR*, DOC fluxes and litter mass loss. Additionally, we traced ^{13}C -labelled litter in leached DOC at site 400. We hypothesized (1) that soil C fluxes would decrease with increasing altitude as a result of a decreasing ecosystem productivity, (2) that summer drought would reduce *SR* and DOC fluxes with the litter-derived fluxes responding more sensitive due to the greater exposure of litter to drying; and (3) that accelerated fluxes after rewetting would at least partly compensate for the suppressed fluxes during drought.

Materials and methods

Study sites and experimental set-up

The field experiments were conducted in three managed grasslands at different altitudes across Switzerland: Chamau (lowland 400 m a.s.l., Huenenberg ZG),

Fruebuel (montane 1,000 m a.s.l., Walchwil ZG) and Alp Weissenstein (alpine 2,000 m a.s.l., Berguen GR). These sites will hereafter be called 400, 1,000 and 2,000. The three grasslands represent the traditional Swiss Alpine farming system (Eugster and Zeeman 2006; Eugster and Leuenberger 2007; Hiller et al. 2008). Climatic conditions and soil properties are given in Table 1.

Drought experiment

For the drought experiment, we first laid out six plots (3 m × 3.5 m) on an area of 25/25 m with 2 m buffer stripes in between individual plots at each of the three sites. The plots were arranged in three pairs of adjacent plots from which one plot was randomly assigned to the unmanipulated control treatment and one to the drought treatment. This resulted in a split-plot design with the three sites as the blocks and the adjacent plots as main plots each with a control and a drought treatment ($n = 3$). To simulate a pronounced summer drought, we installed three portable rain shelters, which were tunnel-shaped steel framed constructions (3 m × 3.5 m) with a maximal height of ~2.1 m. We covered them with transparent greenhouse film (200 μm, Gewächshausfolie UV 5, folitec Agrarfolien-Vertriebs GmbH, Westerburg, Germany) during the entire drought treatment periods. The precipitation falling on the roofs was directed away from the experimental area. We established the drought experiments at the sites 400 and 1,000 end of June 2005 and at site 2,000 in July 2006. All three experiments were continued until the end of 2007. In the experimental year 2007, we installed the rain shelter at sites 400, 1,000 and 2,000 on May 2, 7, and June 20 2007, respectively, based on regional climate model projections (e.g. Frei et al. 2006). The experimental summer drought lasted 69, 74 and 64 days. Before and after the drought period no further treatment was applied. Below the three rain shelters at each site, we determined a core area of 1 m × 2 m, where we performed all measurements to avoid any edge effects. The typical farmyard manure application was not carried out during the whole experiment.

Litter addition experiment

At the sites 400, 1,000 and 2,000, we applied ~700 g m⁻² of dry biomass (~315 g C m⁻²)

Table 1 Site description of grassland sites

	400	1,000	2,000
Political community	Hünenberg, ZG	Walchwil, ZG	Bergün, GR
Coordinates	47°12′37″N, 8°24′38″E	47°6′57″N, 8°2′16″E	46°34′60″N, 9°26′″E
Elevation (m a.s.l.)	393	982	1978
Land management	Intensive grassland	Intermediate grassland	Extensive grassland
Soil type (WRB)	Cambisol ^a	Endogleyic Cambisol ^a	Leptosol
Soil texture (0–10 cm)	Loamy clay ^a	Loamy clay ^a	Humous sandy loam ^b
Soil C (% in 0–10 cm)	3.1 ^a	5.1 ^a	8.6 ^b
Soil N (% in 0–10 cm)	0.3 ^a	0.4 ^a	0.7 ^b
Soil C/N	9.4 ^a	11.2 ^a	12.3 ^b
pH of topsoil (0–10 cm)	5.3 ^a	4.3 ^a	6.3 ^b
Mean temperature (°C) ^c	9.8 ^c	7.7 ^c	2.3 ^c
Precipitation (mm) ^c	1232 ^c	1765 ^c	969 ^c
Rain exclusion – duration (d)	69	74	64
Rain exclusion – amount (mm)	403 ^c	589 ^c	254 ^c
Rain exclusion – amount (%)	33	33	26

^a According to Roth (2006)

^b According to Schärer (2003)

^c According to Zeeman (2008) adapted with data from MeteoSwiss

directly on the soil surface in all litter installations for measuring C fluxes (April 22, 30 and June 12, 2007, respectively), and placed a large mesh size net (mesh size 4 mm) above all installations to prevent wind dispersion and mixing with additional litterfall. For the litter study, we collected litter (mixtures of *Lolium perenne* and *Trifolium repens*) nearby our experimental plots 4–6 weeks before we started the measurement campaigns for SR and DOC at sites 1,000 and 2,000 (March and May 2007, respectively), whereas at site 400 we used mixtures of the same plants, but harvested in a previous free air carbon dioxide enrichment study providing a ¹³C depleted litter material (see below).

Micrometeorological measurements

Micrometeorological variables were measured continuously during the whole year. In 2006 we installed ECHO probes (EC-20 ECH₂O sensors, Decagon Devices Inc., Pullman, WA, USA connected to a CR10X datalogger, Campbell Scientific, Logan, UT, USA) at ~5, 15 and 30 cm depth to measure soil moisture every 10 min at two control and two drought plots ($n = 2$) at each of the three sites. Relative air humidity at 60 cm depth was measured at the same

plots (TRH-100, Pace Scientific Inc., Mooresville, NC, USA). Temperature probes were installed in 2006 ($n = 2$) at the same four plots at each of the three sites to detect soil temperature every 10 min at ~5, 15 and 30 cm depth. At a nearby meteorological station air temperature at 2 m height and precipitation were measured at each of the three sites (HydroClip S3, Rotronic AG, Basserdorf, Switzerland and Type 10116, Toss GmbH, Potsdam, Germany; Zeeman 2008).

Soil CO₂ efflux

Soil CO₂ fluxes (SR) were measured from permanently installed thin-walled polyvinyl chloride respiration collars (diameter 20 cm × 5 cm, 2.5 cm soil depth) in each of the three control and drought plots (total collar $n = 18$) at each site. At the three sites, we measured SR 26, 14 and 7 times between April and December 2007 in biweekly to monthly intervals. Each sampling campaign lasted on average 2–3 h; during which we modified the order of the plots to prevent confounding effects by diurnal trends. The measurement procedure has been previously been described in Joos et al. (2008, 2010). Briefly, SR was

measured using an automated soil CO₂ efflux system (LI-8100, Li-Cor Inc., Lincoln, NE, USA) with a LI-8100-103 survey chamber of 20 cm diameter. We measured *SR* three times for each collar, where each measurement lasted 90 s, followed by a 60 s break between the measurements, during which the chamber was automatically opened to allow replacement of chamber air with ambient air. Measurements were performed between 11:00 and 18:00 h. In order to reduce plant respiration, we cut the aboveground vegetation down to 3 cm above ground level ~24 h before each measurement.

DOC sampling

To sample DOC leached from the litter layer and in the mineral soils, we inserted one thin-walled polyvinyl chloride frame (40 cm × 40 cm × 10 cm) to a depth of 2 cm in each of the plots to which we added defined amounts of grassland litter. Within this litter frames, we collected litter leachate with zero tension lysimeters (15 cm × 15 cm × 3 cm) directly inside the litter layer. Soil solution at 5 cm soil depth in the A horizon was sampled with one horizontally installed glass suction plate in each plot (diameter 80 mm, ecoTech, Umweltmesssysteme GmbH, Bonn, Germany). Each sampling device was connected to 1 L glass bottle buried in the soil. The suction plates were continuously evacuated to 400 hPa with a vacuum pump (ecoTech, Umweltmesssysteme GmbH, Bonn, Germany). Prior to the installation of the plates, we flushed them with 1 M HCl and distilled water.

To quantify the contribution of litter-derived DOC to DOC leaching at site 400, we divided each plot in two sub-plots, and thus, installed 12 containers with each having one suction plate and zero-tension lysimeter. In these sub-plots, we either added ¹³C-depleted (-37.2 ± 0.1 ‰ vs. Vienna Pee Dee Belenite (V-PDB)) or reference litter (-27.9 ± 0.1 ‰ vs. V-PDB), both mixtures of *Lolium perenne* and *Trifolium repens* harvested in a previous free air carbon dioxide enrichment study (Hebeisen et al. 1997).

During the rainfall exclusion, soil water sampling was not possible in the drought plots at 400 and 2,000; only at the relatively moist site 1,000, soil solution at 5 cm depth could be collected.

Overall, we sampled DOC 11, 9 and 5 times between April and December 2007 (for each campaign

$n = 3$ per drought treatment) at sites 400, 1,000 and 2,000 in biweekly to monthly intervals. All soil water samples were stored in cooling boxes for the transport to the laboratory, then filtered using 0.45 μm polycarbonate membrane filters, and finally stored at 2 °C until measurement.

Litter decomposition

We studied litter decomposition using the most widely applied litterbag method (Bocock and Gilbert 1957). Litter (mixtures of *Lolium perenne* and *Trifolium repens*) was collected nearby our experimental sites before we started the measurement campaigns for *SR* and DOC leaching (March–May 2007). Before filling the litterbags, the litter mixtures were oven-dried (65 °C) to constant weight. For each of the three drought and control plot, five litterbags (10 cm × 10 cm, Polyester fibre material, mesh size 1 mm, SEFAR AG, Thal, Switzerland) were filled with ~2 g of litter mixture (total $n = 90$ litterbags, 30 per site). The small mesh size was chosen to minimize losses of litter due to breakage—a recognized bias of the litterbag technique (Loranger et al. 2002).

At the beginning of the vegetation period the litterbags were randomly placed onto the ground of the plots, in April 2007 at sites 400 and 1,000, and in June 2007 at site 2,000. They were secured with wire hooks to ensure close contact with the soil. The in situ litter was removed before placement. We collected three litterbags per treatment directly after the drought treatment (July 2007 at sites 400 and 1,000 and in August 2007 at site 2,000) and in monthly intervals until December, November and October 2007 (229, 193, and 137 days post-exposure). Collected litterbags were carefully transferred into individual plastic bags and transported to the laboratory. Remaining litter was thoroughly cleaned with fine brushes from extraneous material (adhering plants, plant debris, and soil). The residual weight of the cleaned litter was recorded after oven-drying at 65 °C to constant weight.

Chemical analyses of leachates and litter

We determined DOC concentrations with a Shimadzu TOC/TN analyser (TOC-V, Shimadzu Corporation, Tokyo, Japan). Subsequently, the molar UV absorptivity at 285 nm in DOC was measured as a measure for aromaticity and the so-called “hydrophobic” DOC

(Kalbitz et al. 2003; Dilling and Kaiser 2002) with a Cary 50 UV spectrophotometer (Varian, Incorporated, Palo Alto, California, United States). To estimate the fraction of ‘new’ litter-derived C in DOC, we analysed the $\delta^{13}\text{C}$ values of DOC fractions by freeze-drying aliquots. Prior to the freeze-drying we added small amounts of K_2SO_4 to facilitate the recovery and weighing of samples. The C isotope analyses were performed with an automated elemental analyser-continuous flow isotope ratio mass spectrometer (EA-1110, Carlo Erba, Milan, interfaced with a Delta-S Finnigan MAT, Bremen). Results of ^{13}C analyses are expressed in δ U (%), the $\delta^{13}\text{C}$ values were referenced to the Vienna Pee Dee Belemnite (V-PDB) standard.

The dried litter samples were first milled and then C and N concentrations were measured with a CHN analyser (Model 900, LECO Instruments, St. Joseph, Mich., USA).

Estimation of soil carbon fluxes and temperature dependency

Temperature dependencies of *SR* from control plots were estimated by the Q_{10} function:

$$SR = R_{10} \times Q_{10}^{((T-10)/10)} \quad (1)$$

in which R_{10} is the respiration rate at 10 °C, Q_{10} is the temperature sensitivity (over a range of 10 °C), and T is the soil temperature at 5 cm depth. The R_{10} and Q_{10} were estimated by fitting measured data using the Levenberg–Marquardt algorithm (Origin 7.0, Origin-Lab). Because the litter-derived component had an overarching effect on *SR* rates directly after the litter addition, we estimated the temperature dependencies for “belowground *SR*”, where the litter-derived component was subtracted from the measured *SR* rates. To do so, we first fitted litter mineralization (=litter mass loss – DOC leaching from the litter) to a one exponential decay function [$y = a + b \times \exp(-kt)$]. The fitted total litter mineralization corresponded closely to respiratory C losses estimated using the ^{13}C label of the added litter at the site 400 (0.26 vs. 0.27 kg C m^{-2} ; Joos et al. 2010). In a second step, the estimated litter mineralization rates were subtracted from measured *SR*.

Fluxes of *SR* were calculated by interpolating linearly between two measurements and integrating over the respective period. As *SR* measurements were

carried out during the warmer daytime we adjusted *SR* measured at a given temperature to monitor mean daily temperatures by applying the estimated temperature dependency of *SR*.

Fluxes of DOC were estimated by multiplying DOC concentrations with water fluxes modelled with the ecosystem model COUP (Jansson and Karlberg 2004). The basic structure of the model is a depth profile of the soil and the calculations of water flows are based on common soil properties, e.g. the water retention curves. The model is driven by meteorological data with precipitation, air temperature, wind speed, air humidity and radiation as a minimum input data set for which we had hourly data from nearby meteo stations. Soil hydraulic properties were generally inferred from measured texture parameters, using built in pedotransfer functions calculating water retention curves and saturated/unsaturated conductivities. As we had no profile data for site 2,000, soil hydraulic parameters were adjusted manually referring to the dominant soil type present at this site (Table 1). A basic quality check of individual model runs was provided by the accumulated water balance and measured soil water contents. Model output included soil moisture and water flows in various depths as well as interception and water balance terms in daily resolution.

The fraction of new C in DOC derived from freshly added litter in % was calculated as follows:

$$\text{DOC}_{\text{new}} = 100 \times \frac{(\delta^{13}\text{C}_{\text{DOC,depleted}} - \delta^{13}\text{C}_{\text{DOC,ambient}})}{(\delta^{13}\text{C}_{\text{Litter,depleted}} - \delta^{13}\text{C}_{\text{Litter,ambient}})} \quad (2)$$

where $\delta^{13}\text{C}_{\text{DOC,depleted}}$ is the $\delta^{13}\text{C}$ in DOC from the plots with depleted litter, $\delta^{13}\text{C}_{\text{DOC,ambient}}$ is the $\delta^{13}\text{C}$ in DOC from the plots with ambient litter and $\delta^{13}\text{C}_{\text{Litter,depleted}}$ is the average $\delta^{13}\text{C}$ of the depleted litter mixture. The flux of new DOC was calculated by multiplying fraction of new C with DOC fluxes.

Statistical analysis

We analyzed our data by fitting mixed-effects models by maximum likelihood [lme function from the nlme package, R 2.10.1, R Development Core and Team (2010)]. The models included the sequential fixed effects site, treatment (control vs. drought; $n = 3$ per site), and day accounting for the split-plot design and

repeated measurement structure. Residuals of repeated measures showed a first-order autoregressive covariate structure, which was included in the model using the *corAR1* function. In additional analyses, we analyzed the data for the drought and post-drought period and for the sums of the different periods. In all final models, normality and homoscedasticity of the residuals were verified visually with diagnostic plots and, when necessary, the dependent variable (e.g. soil CO₂ efflux) were log transformed.

Results

Drought simulation

Annual rainfall in 2007 amounted to 1,232, 1,765 and 969 mm at the sites 400, 1,000 and 2,000, respectively

(Zeeman 2008; adjusted data from nearby MeteoSwiss stations). The installation of rain shelters for 64–74 days decreased precipitation by 403, 589 and 254 mm at the three altitudes, which corresponded to a reduction of annual rainfall by 33, 33 and 26 % at the sites 400, 1,000 and 2,000, respectively (Fig. 1; Table 1). Soil water contents at 30 cm depth decreased by 69–22 % during the drought period, with the smallest decline at site 1,000 where soils showed signs of temporary water logging. Two weeks after the drought, soil water contents in the drought plots increased back to the values of the control plots at sites 400 and 1,000. Due to technical problems at site 2,000, no continuous data was available, but gravimetric soil water contents in 0–5 cm depth at the end of the drought treatment showed a 41 % reduction in soil moisture under drought ($P < 0.001$; Gilgen and Buchmann 2009). In agreement with measured values at the

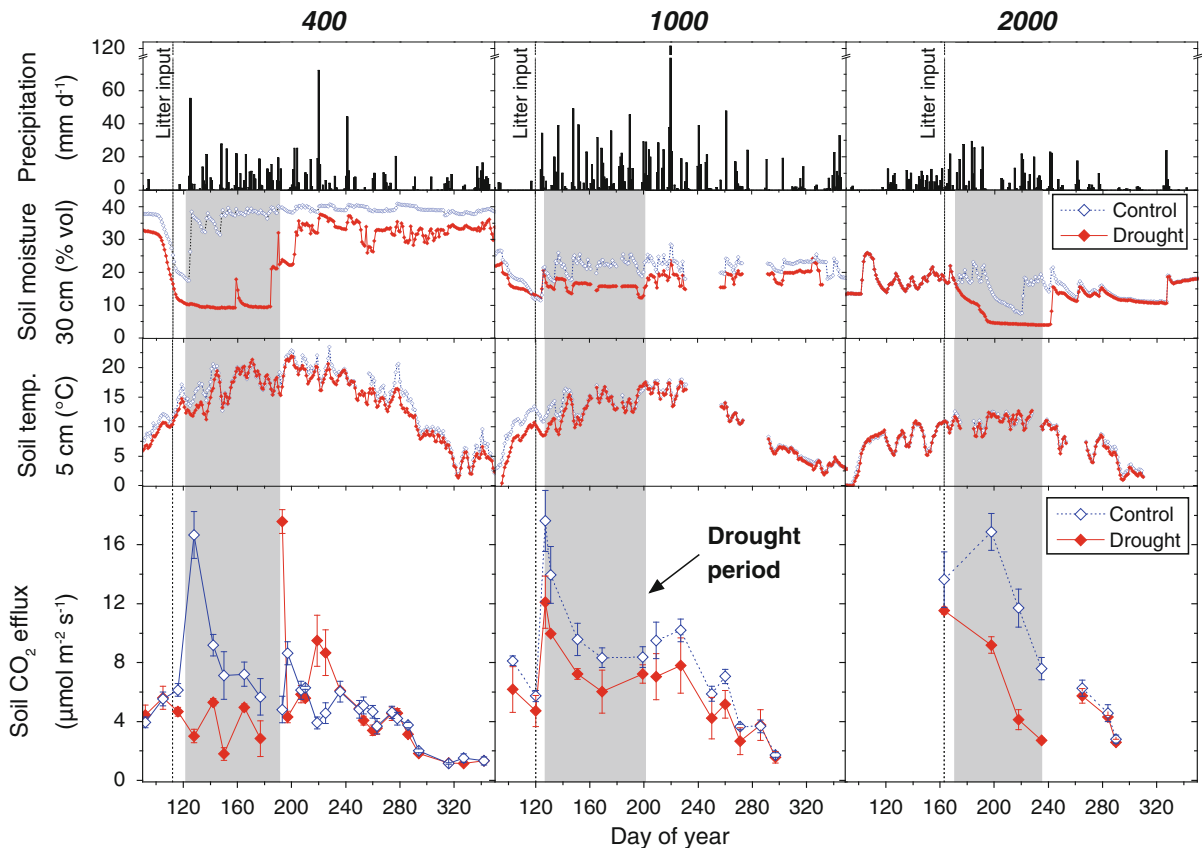


Fig. 1 Precipitation, soil volumetric water contents, soil temperature, and soil CO₂ efflux measured in control and drought plots at sites 400, 1,000 and 2,000 during the litter addition experiment in 2007. Daily ambient precipitations from adjacent meteorological stations (Zeeman et al. 2010). Daily

volumetric soil moisture at 30 cm depth. Daily soil temperature at 5 cm depth. Soil CO₂ effluxes measured biweekly. Means and standard errors for soil CO₂ effluxes $n = 3$, for soil temperature and moisture $n = 2$

two lower sites, modelling of soil water contents using COUP also showed a recovery to control plot levels after 2 weeks (data not shown). Measured relative air humidity was high with average values of 83, 89 and 76 % at the sites 400, 1,000 and 2,000 during the time when roof had been installed (data not shown). These values were not systematically affected by the roofs with small changes of 2.9 ± 4.1 , -5.6 ± 6.7 and 1.7 ± 3.7 (mean \pm SD) at the sites 400, 1,000 and 2,000. Average soil temperatures at 5 cm soil depth were 13.9, 10.4, and 7.8 °C at sites 400, 1,000 and 2,000 during the 250 day long measurement period. Air and soil temperature were not significantly affected by the drought treatment.

Soil CO₂ effluxes at different altitudes

Soil CO₂ effluxes (*SR*) at all three altitudes showed a strong peak shortly after litter addition with rates of up to $18 \mu\text{mol m}^{-2} \text{s}^{-1}$, leveling off during the following 2 months (Fig. 1). Due to the overarching effect of the added litter, total *SR* rates did not significantly correlate with soil temperatures. However, when fitted litter mineralization was subtracted from these values, belowground *SR* of control plots showed a close relationship with soil temperatures for each site ($r^2 = 0.87\text{--}0.97$, $P < 0.001$; Fig. 2) but not with soil moisture. Although temperature decreased with

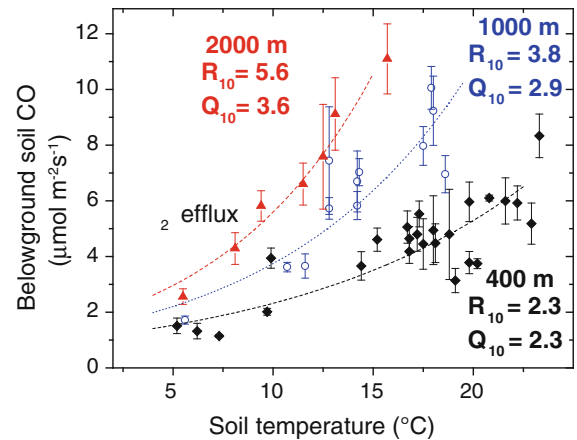


Fig. 2 Relationship between soil temperatures and belowground soil CO₂ effluxes estimated by subtracting fitted litter mineralization from measured soil respiration. The R_{10} and Q_{10} values are fitted values from the Q_{10} function ($SR = R_{10} \times Q_{10}^{((T-10)/10)}$, where R_{10} is the soil CO₂ efflux at 10 °C and the Q_{10} is the temperature sensitivity over a range of 10 °C. The r^2 values of the fitted curves are 0.87 for the sites 400 and 1,000 and 0.97 for the site 2,000. Means and standard errors of three plots per treatment

increasing altitude, soil CO₂ effluxes (*SR*) of the control plots were not significantly different between the sites ($P_{\text{site}} > 0.05$; Fig. 1; Table 2). This indicates that at a given soil temperature *SR* was higher at greater altitudes. Accordingly, the fitted R_{10} values of belowground *SR* Eq. (1) increased with altitude from

Table 2 Statistical significances of the linear-mixed model testing the effects of site and drought on soil CO₂ efflux and DOC concentrations and of residual litter carbon during and after the drought periods as well over the full experimental period in 2007

The experimental drought was carried out with three rainout shelters and adjacent control plots at three sites (400, 1,000 and 2,000)

nd not determined, no samples

*** $P < 0.001$; ** $P < 0.01$;

* $P < 0.05$

	CO ₂ efflux	DOC concentration		Litter C
		Litter layer	A horizon	
Drought period				
Site	0.60	nd	nd	0.08
Drought	<0.001***	nd	nd	<0.001***
Site \times drought	<0.04*	nd	nd	0.002**
Post-drought				
Site	0.53	0.65	0.87	0.09***
Drought	0.06	<0.001***	0.80	<0.001***
Site \times drought	0.34	0.10	0.38	0.007**
Drought \times time	0.62	0.003**	0.04*	0.18**
Site \times drought \times time	0.006**	0.26	0.32	<0.001***
Experimental period				
Site	0.10	0.77	0.78	0.05*
Drought	<0.001***	<0.001***	0.86	<0.001***
Site \times drought	<0.001***	0.68	0.46	0.44
Drought \times time	0.08	0.34	0.002**	<0.001***
Site \times drought \times time	0.78	0.02*	0.80	0.007**

2.3, 3.8 to 5.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the sites 400, 1,000 and 2,000, respectively (Fig. 2).

Drought effects on soil CO_2 effluxes

The experimental drought significantly affected SR , but the direction of the response was different for the drought period and the time thereafter ($P_{\text{drought} \times \text{date}} < 0.001$). Rain exclusion decreased SR at all sites during the drought periods ($P_{\text{drought}} < 0.001$); the decline was largest at site 400 and 2,000 (-57%) and smallest at site 1,000 (-25% ; Table 3). After rewetting, the responses of SR differed strongly among the sites ($P_{\text{site} \times \text{drought} \times \text{date}} < 0.01$; Table 2). At site 400, SR of the former drought plots increased during the following month ($P_{\text{drought}} < 0.05$) and declined thereafter, while at site 1,000, SR remained lower except the last two sampling dates. At site 2,000, SR returned to the same rates as in the control; however, as the first post-drought measurement was carried out 23 days after the drought, there might have been a transient response before. Integrated over the full experimental period, drought decreased SR by 16–39%, but the effect was only significant at site 2,000. In absolute terms, the cumulated SR of the control plots amounted to 1,080–1,500 $\text{g CO}_2\text{-C m}^{-2}$ and the experimental drought decreased it between 200 and 420 $\text{g CO}_2\text{-C m}^{-2}$ ($P_{\text{drought}} < 0.001$; Table 3). The absolute effect of the drought would very likely have been similar on an annual time scale, as SR did not differ between the treatments at the last measurements of the season.

Dissolved organic carbon

Concentrations of DOC were much higher under the litter layer than in the soil solution at 5 cm depth in the A horizon directly after the litter addition (Fig. 3). The difference in DOC between the two depths, however, declined throughout the growing season. DOC concentrations of the control plots under the litter layer and at 5 cm depth differed not significantly among sites ($P_{\text{site}} > 0.70$; Table 2). The experimental drought prevented water fluxes during the drought periods and hence, DOC was not measurable at this time. However, directly after the drought, DOC concentrations under the litter layer were 2–8 times higher in the drought than in the control plots

($P_{\text{drought}} < 0.001$), but this effect decreased with time ($P_{\text{drought} \times \text{time}} < 0.003$). At 5 cm depth in the mineral top soil, this initial increase in DOC concentrations was smaller ($+50\%$; $P_{\text{drought} \times \text{time}} < 0.04$).

Cumulated DOC fluxes were more than an order of magnitude smaller than soil CO_2 effluxes (Tables 3, 4). As expected, DOC fluxes were negligible during the drought due to the cessation of water fluxes. After the drought, DOC fluxes under the litter layer increased by 6 and 9 g C m^{-2} at the sites 2,000 and 400 and even by 30 g C m^{-2} at site 1,000 (Table 3) due to high rainfalls and higher DOC concentrations as compared to the control (Fig. 3; $P_{\text{Drought, all sites}} < 0.02$). However, this increase did not compensate for the reduced DOC leaching during the drought period at the sites 2,000 and 400. Thus, the overall decrease in DOC leaching over the full experimental period amounted on average to 15 g C m^{-2} (-34% ; $P_{\text{Drought, all sites}} < 0.05$). At 5 cm depth, the rewetting effect was negligible and consequently the drought decreased total DOC leaching by 12 g C m^{-2} (-60% ; $P_{\text{Drought}} < 0.001$).

The specific UV absorbance ($SUVA$) as an indicator for the aromaticity and contents of the so-called “hydrophobic” DOC (Dilling and Kaiser 2002), increased during the first 2 months after litter addition but remained constant thereafter (Fig. 4). The increase in $SUVA$ was delayed with smaller values directly after the drought under the litter layer and in the A horizon (Fig. 4; $P_{\text{Drought}} < 0.05$).

Our ^{13}C tracer study at site 400 provided insight into the sources of DOC. The ^{13}C signal of the ^{13}C -depleted litter ($\Delta^{13}\text{C} = \delta^{13}\text{C}_{\text{depleted}} - \delta^{13}\text{C}_{\text{ambient}}$) was significantly reflected in DOC, with $\Delta^{13}\text{C}$ ranging between -8.3 and -0.1% , but declined with time (data not shown). On average, 78 and 16% of the DOC under the litter layer and in the A horizon of the control plots were derived from the applied litter during the 250 day long measurement period. The experimental drought strongly decreased litter-derived DOC leaching ($P < 0.05$; Fig. 5). Under drought, litter-derived DOC leaching amounted only to 3 and 8% of the one of the control plots. This decrease was stronger than for total DOC concentration, which implies that drought led to smaller fractions of litter-derived DOC. Hence, the relative contributions to DOC leaching from other sources, such as leaching from plant tissues and indigeneous SOM increased (Fig. 5).

Table 3 Effects of experimental drought on the cumulated soil CO₂ effluxes linearly interpolated between measurements. Fluxes and drought effects are shown for the drought period (69, 74 and 64 days) and the full experimental period (251, 210

and 137 days) at sites 400, 1,000 and 2,000, respectively. Effect (%) = 100*(Drought-Control)/Control; $n = 3$ per site and treatment

	Cumulated soil CO ₂ efflux (g CO ₂ -C m ⁻²)								
	400			1,000			2,000		
	Control	Drought	Diff. (%)	Control	Drought	Diff. (%)	Control	Drought	Diff. (%)
Drought period	470	200	-57*	640	480	-25*	680	290	-57***
Experimental period	1,250	1,040	-17	1,500	1,150	-24	1,080	670	-38**

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$

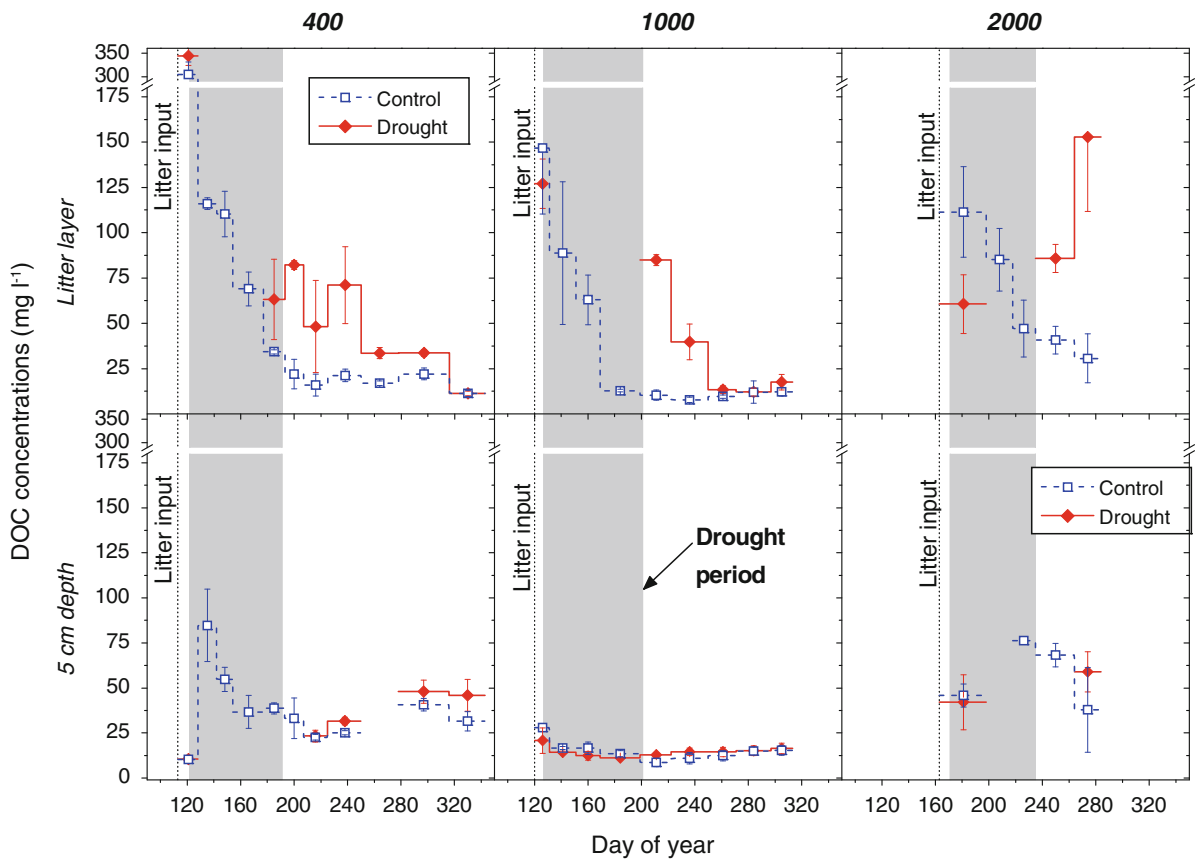


Fig. 3 Effects of experimental drought on DOC concentrations under the added litter and at 5 cm soil depth at sites 400, 1,000 and 2,000 during the litter addition experiment in 2007. Means and standard errors of three plots per treatment

Litter decomposition

Litter C mass loss of control plots increased with decreasing altitude (Fig. 6; $P_{\text{site}} = 0.02$) with around 4, 11 and 22 % of the initial litter C remaining after 137 days in the field at sites 400, 1,000 and 2,000, respectively. Drought had a strong effect on litter

decomposition with seven, six, and two times more litter remaining under the experimental roofs after the drought period ($P_{\text{Drought}} < 0.001$). The litter mass loss increased after the removal of the roofs. At the end of the season, the remaining litter masses were low at all sites, but significantly smaller in the drought treatment ($P < 0.05$).

Table 4 Effects of experimental drought on cumulated DOC fluxes under the added litter layer and at 5 cm depth in the mineral soil. Fluxes and drought effects are shown for the drought period (69, 74 and 64 days) and the full experimental

period (251, 210 and 137 days) at sites 400, 1,000 and 2,000, respectively. Effect (%) = 100 × (drought – control)/control; n = 3 per site

		Cumulated DOC flux (g DOC m ⁻²)								
		400			1,000			2,000		
		Control	Drought	Diff. (%)	Control	Drought	Diff. (%)	Control	Drought	Diff. (%)
Litter layer	Drought period	44.9	1.1	−98***	33.4	7.1	−79*	28.5	2.3	−92*
	Experimental period	53.4	24.3	−55**	40.2	45.5	13	32.3	12.1	−63
A horizon	Drought period	16.9	0	−100***	8.7	1.2	−86*	13.0	0.9	−93**
	Experimental period	28.8	12.2	−58***	15.4	9.0	−42	20.3	3.8	−81**

***P < 0.001 ; **P < 0.01 ; *P < 0.05

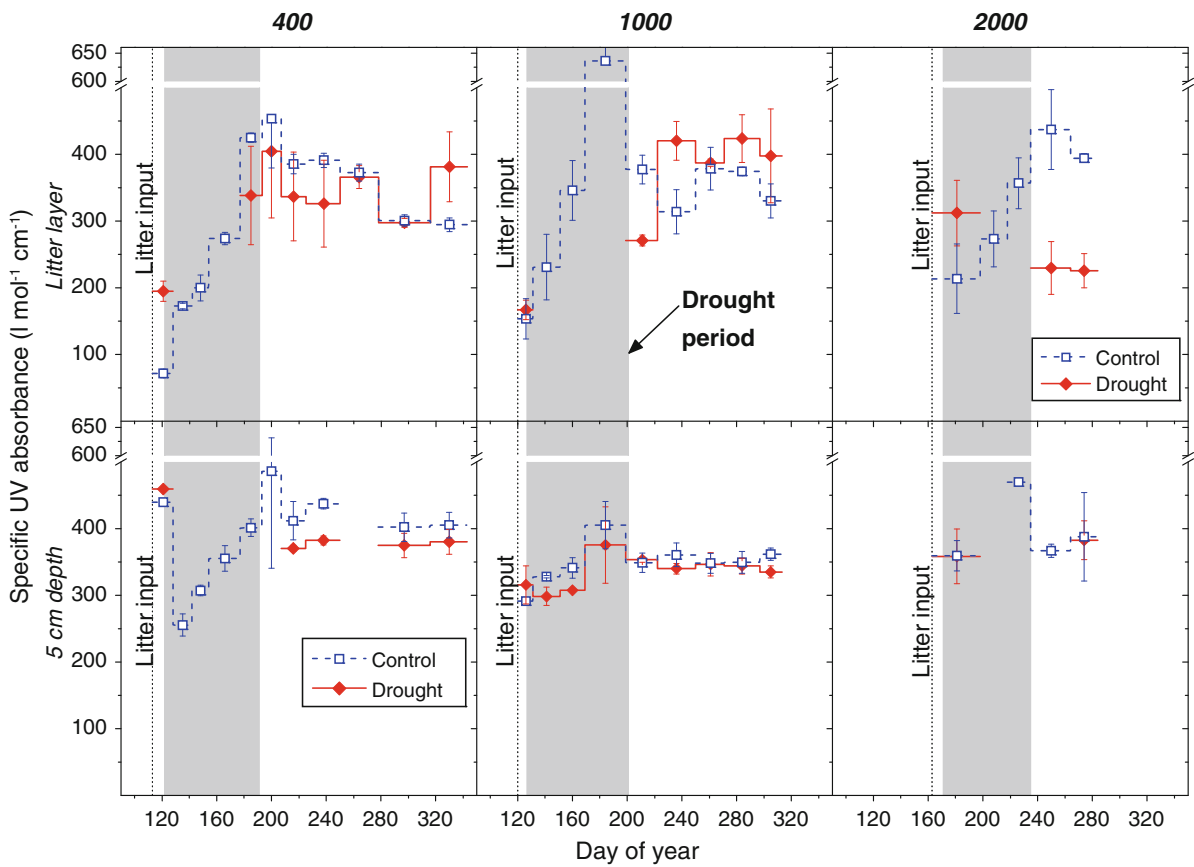


Fig. 4 Effects of experimental drought on the specific UV absorbance at 285 nm under the added litter and at 5 cm depth in the A horizon at the sites 400, 1,000 and 2,000. Means and standard errors of three plots per treatment

Discussion

Soil CO₂ and DOC fluxes at three altitudes

The SR rates reaching 15–18 μmol CO₂ m⁻² s⁻¹ at our sites are among the highest observed in any kind of

ecosystem (Bahn et al. 2008). These exceptionally high fluxes can partly be attributed to the high decomposition rates of the added grass litter. For the lowest site at 400 m a.s.l., the labelled litter experiment indicated a litter contribution of about 50 % directly after litter addition in early summer, which

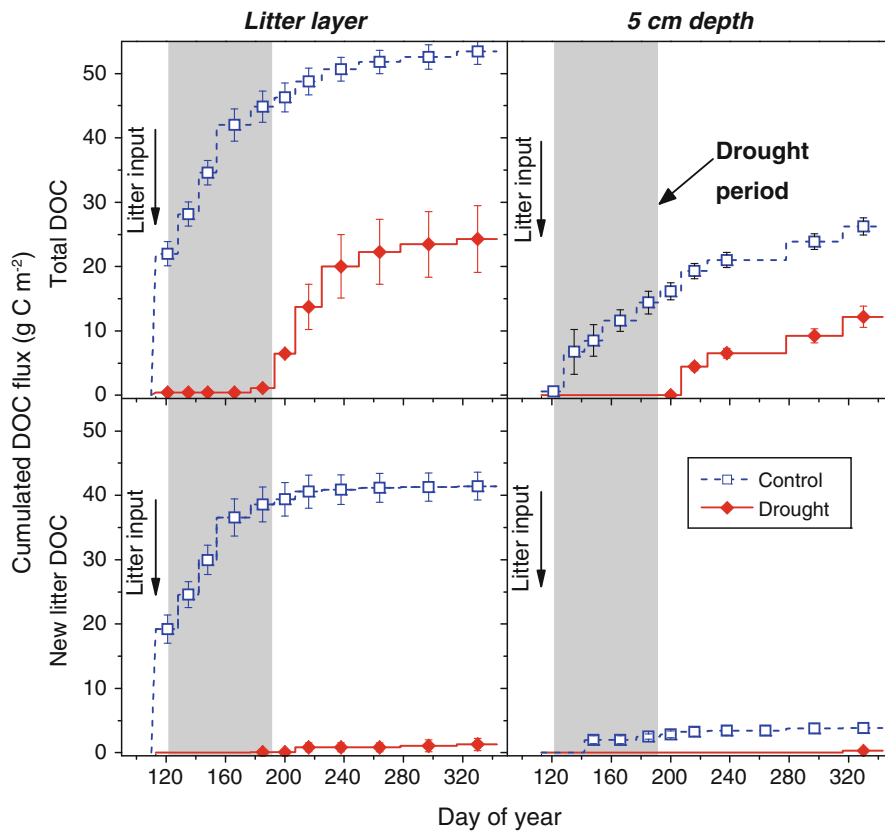


Fig. 5 Effects of experimental drought on cumulated fluxes of total DOC and of “new” litter-derived C under the added litter and at 5 cm depth at the site 400. The new litter DOC was

estimated from tracking ^{13}C depleted litter in leached DOC. Means and standard errors of three plots per treatment

decreased to 10 % within the next two months (Joos et al. 2010). In agreement with our values, a number of Central European grasslands showed similarly high maximal SR rates of 14–16 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and annual soil CO_2 effluxes of up to 2000 $\text{g CO}_2\text{-C m}^{-2} \text{ year}^{-1}$ (Bahn et al. 2008). Also, eddy covariance measurements at the two lower grassland sites 400 and 1,000 showed a very high annual ecosystem C assimilation with 1,900 to 2,700 $\text{g C m}^{-2} \text{ year}^{-1}$ and ecosystem respiration of 1,560–2,650 $\text{g C m}^{-2} \text{ year}^{-1}$ (Zeeman et al. 2010), indicating that temperate grasslands are extremely productive ecosystems with very high C cycling rates, probably due to an optimal nutrient supply through long-lasting fertilization, ideal soil moisture status and favorable climatic conditions.

Interestingly, SR rates did not decline with increasing altitude, although soil temperatures decreased by about 5 °C across the 1,500 m in elevation, showing that at a given soil temperature SR strongly increased

with increasing altitude. The lacking relationship of SR with temperature across sites can either be interpreted as a “thermal” adaptation of ecosystems in a warmer climate, homeostasis (e.g. Bradford et al. 2008) or due to a substrate depletion in a warmer climate and hence at lower altitude (Eliasson et al. 2005). The “thermal” adaptation could include an increasing C allocation to the belowground C with decreasing temperatures in relative, but even in absolute terms. For instance, based on ingrowth cores, Gilgen and Buchmann (2009) observed a doubling of belowground biomass productivity in our field experiment. The second reason for the insignificant effects of temperature on SR across sites is a higher substrate availability in soils in a colder climate due to a slower decomposition of litter and SOM. Indeed, soil C contents of the topsoils almost tripled from the lowest to the highest site (Table 1), which is in line with the observed increase of soil C contents with increasing

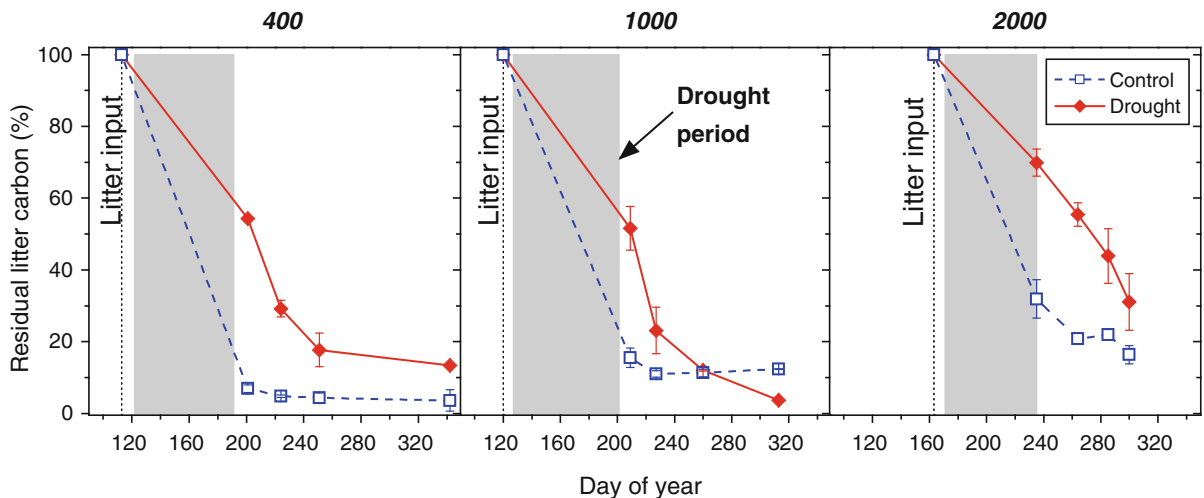


Fig. 6 Effects of experimental drought on remaining litter C in litterbags at the sites 400, 1,000 and 2,000 in 2007. Means and standard errors of three plots

altitude in Swiss grasslands in a more extensive soil survey including more than 500 soils (Leifeld et al. 2005). Moreover, Leifeld et al. (2009) found increasing fractions of particulate and hence “labile” soil organic carbon (SOC) with increasing altitude. In our study, the increased C/N ratios at the higher sites also suggest higher proportions of less decomposed, and thus more readily available SOC. In agreement with our grassland study, Caprez et al. (2012) have observed similarly high *SR* rates across a 1,000 m elevational gradient in Swiss forest soils. Also, Zimmermann et al. (2009) did not find a significant relationship of heterotrophic respiration with elevation along a 3,000 m altitudinal gradient in the tropics when daytime data were compared. Our litter decomposition study supports substrate depletion as the primary reason for the lacking elevational decline in *SR*. In contrast to total *SR*, litter mass loss, and hence, the decomposition of an identical labile substrate increased with decreasing altitude and reflected an accelerated turnover of a given organic material at increased temperatures.

The fluxes of DOC in the litter layer were about an order of magnitude smaller as compared to respiratory C losses. Concentrations and fluxes were similar to those of a monitoring study across different European ecosystems (Kindler et al. 2010), showing that DOC fluxes can be equally high in forests. Although DOC fluxes are substantially smaller than *SR*, they can be important for the net ecosystem C balance; in

particular because they transport C to deeper soil horizons (Kaiser and Kalbitz 2012). Our tracer study with ^{13}C -depleted litter indicated a rapid retention of “new” litter-derived DOC in the mineral soil and a concomitant generation of “older” DOC in the A horizon. This DOC pattern is consistent with the increasing ^{14}C age observed in grasslands (Sanderman and Amundson 2008). Here, we cannot elucidate if the retention of litter DOC was primarily related to biodegradation (and hence a loss of litter C) or to physico-chemical sorption (and thus, a C stabilization). However, the tracer experiment by Müller et al. (2009) with ^{13}C -labelled DOC leached from spruce litter indicated that sorption was the primary retention mechanism in surface soils suggesting a long-term stabilization of this small litter-derived component.

Drought effects

Our experimental set-up resulted in a realistic reduction in summer rainfall by 30 % similar to natural droughts such as in the year 2003 (Ciais et al. 2005). As expected, the drought decreased soil C fluxes at all sites, which is consistent with other drought experiments in mesic and dry environments (Borken et al. 2006; Harper et al. 2005; Muhr and Borken 2009). We expected that the magnitude of the drought response would decrease with increasing altitude because soil water losses are smaller at lower temperatures. However, we observed the smallest *SR* reductions

under drought at the intermediate site *I,000*, which we attribute to the gleyic soil properties with high antecedent water contents that are typical for many soils of the Pre-Alps, (unintended) lateral water flow under the roofs because this site had the steepest slopes and the highest annual rainfall. The site *I,000* also experienced the smallest reduction in soil water contents (Fig. 1) and showed no drought response of plant growth (Gilgen and Buchmann 2009).

Leaching of DOC responded more sensitive to the experimental drought than *SR*, which contrasts with the drying and rewetting experiments with forest floors in the laboratory by Muhr et al. (2010) showing that extended drought decreased *SR*, but had little impacts on DOC concentrations. However, in their experiment, Muhr et al. (2010) kept soil moisture constant in the control treatment and thus, prevented leaching during the drought period, which would have increased DOC fluxes in the control as compared to the drought. In our field study, we attribute the stronger drought effect on DOC fluxes than on *SR* to the fact that water drainage ceases at comparatively higher soil moisture contents than microbial activity. Consequently, during soil drying, at least during the initial phase, solublizable C is not leached but mineralized. Since the strong drought effect on DOC fluxes can be ascribed to the cessation of water fluxes and not to changes in DOC concentrations, we think that the magnitude of the drought effect most strongly depends on the effect on water fluxes and not on an altered DOC production.

Our study gives no strong support for the ‘Birch’ effect, the mineralization flush upon rewetting. Only at site *400*, *SR* increased directly after the drought, but we cannot rule out that we might have missed a very short-lived mineralization flush. However, temporarily highly resolved monitoring of soil CO₂ effluxes in the laboratory by Muhr et al. (2010) revealed only a less than 30 %-increase for about 10 days following a very severe drought, which would have not been quantitatively important for C losses on a seasonal and annual basis. Moreover, we also only observed insignificant 17 %-increase in DOC concentrations at 5 cm soil depths at the three sites, where we would have captured any additionally released DOC by the continuous application of a vacuum to the suction plates sampling soil solution. The only soil C flux for which we have observed a strong increase following rewetting, was DOC leached from the litter layer.

Here, however, a delayed litter decomposition and hence a higher availability of solublizable substrate might have contributed to this DOC increase. In addition, physical disruption of plant litter structures and the leaching of lysed microbial biomass might have contributed to the post drought peak. Though, as the DOC flush did by far not exceed the initial peak after litter addition and hence, did not compensate for the reduced leaching during the drought itself, it seems unlikely that there was a large release of additional C beyond a preservation of substrate. The measurement of the specific UV absorbance (SUVA) support our conclusion. Lysed microbial and plant cells released after drought typically consist of carbohydrates, which have a very low SUVA due to the lack of aromatic structures (Kalbitz et al. 2003; Fröberg et al. 2007). In our study, SUVA was indeed lower after the drought, particularly under the litter layer (Fig. 4). However, SUVA did not drop to values below the ones after the litter addition before the drought, indicating that if there was cell lysis, it did not lead to a stronger DOC release than from fresh litter.

The litter decomposition experiment and the tracking of ¹³C-labelled litter in DOC both indicated that the experimental drought has altered the sources of soil C fluxes. Drought decreased litter decomposition during the drought more strongly than *SR* and prevented the leaching of litter-derived DOC at 5 cm soil depth. In our experimental drought using permanently installed roofs, we might have underestimated the drought effect on litter-derived C fluxes because air humidity remained similarly high under the roofs than in the control plots (on average > 75 % rH), probably providing sufficient moisture for a reduced but ongoing microbial activity (Dirks et al. 2010), while during a “natural” drought, air humidity decreases strongly (Rebetez et al. 2006). The evident reason for the greater susceptibility of C fluxes to drought in the litter layer than in the mineral soil is the more rapid drying of the litter at the soil surface (Joos et al. 2010). However, in their recent review, Manzoni et al. (2012) pointed out that microbial activity ceases at more negative water potentials in the surface litter than in the mineral soil, because it is dehydration rather than solute diffusion that probably limits biological activity around the stress point in litter, while substrate diffusion and hence availability becomes limiting in the mineral soil. Despite the more negative threshold in the litter, it seems likely that decomposition of litter

responds more sensitive to drought than heterotrophic mineralization in the deeper soils, as litter residues are spatially disconnected from the soil pore system and dry out much more rapidly.

Drought effects on ecosystem C balance

Our results showing strong reductions of litter-derived fluxes and a comparatively smaller decrease of total *SR*, integrating across the whole soil profile indicates that drought altered the sources of soil C fluxes with a preservation of C in topsoils but an ongoing loss of C from the subsoils. Unfortunately, we could not estimate if the reduced *SR* was related to a suppressed root respiration or to SOM mineralization. Radiocarbon and ^{13}C based tracer studies observed ambiguous effects on root respiration with drought responses reaching from declining to increasing contributions of roots to *SR* (Muhr and Borken 2009; Ruehr et al. 2009; Sanaullah et al. 2012). In our field experiment, root biomass was not affected by the drought, which would rather suggest a smaller response of root respiration than of SOM mineralization. However, independent of the drought responses of auto and heterotrophic respiration, we presume that the impacts of drought on SOM mineralization decline with soil depths due to a stronger drying of topsoils during seasonal droughts. An ongoing SOM mineralization in the deeper soil would imply a stronger loss of ‘older’ soil carbon under drought, which is supported by increasing ^{14}C ages of heterotrophically respired CO_2 in drying forest soils (Muhr and Borken 2009). A declining transport of ‘new’ DOC into the deeper soil would amplify a C accumulation in topsoils, but also losses of probably ‘older’ C in subsoils under drought.

In addition to the responses of soil C fluxes, drought effects on net C balance depends on C uptake by plants. In our field experiments, biomass responses differed among the three altitudes. While drought reduced total plant productivity by about 150 and 70 $\text{g C m}^{-2} \text{ year}^{-1}$ at the sites 400 and 2,000, it did not affect productivity at site 1,000 (Gilgen and Buchmann 2009). Here, we observed reductions in *SR* of 160–440 $\text{g CO}_2\text{-C m}^{-2} \text{ year}^{-1}$ which clearly exceeded the decreases in biomass production at all three sites, indicating that the experimental drought led to overall C gains in the ecosystems. Our experimental findings contradict eddy-covariance measurements in North America and Europe showing

a reduced net ecosystem C uptake during extremely dry years and extended droughts as ecosystem respiration decreases less strongly than C uptake under drier conditions (Ciais et al. 2005; Schwalm et al. 2012; Scott et al. 2009). One reason for the opposite response might be that in our study, the experimental droughts of 64–74 days were too short to suppress growth of deep-rooting grasses in the otherwise moist soils under a normally moist climate. By contrast, *SR* became rather rapidly moisture-limited in surface soils.

Conclusions

Contrary to our expectation, *SR* rates did not decrease with increasing altitude and hence they were higher at a given temperature at higher altitudes, which we primarily relate to a greater substrate availability in soils and an increased belowground biomass production observed under a colder climate. The experimental simulation of expected summer droughts significantly reduced *SR*, DOC leaching and litter decomposition at all altitudes, indicating that grassland soils in Switzerland are highly sensitive to changes in soil moisture. We did not observe a strong mineralization flush upon rewetting. Results showed that *SR* in the litter layer was more sensitive to drought than in the deeper soil. In conjunction with the declining fluxes of total and litter-derived DOC, these findings imply a SOC preservation in topsoils, but ongoing losses of probably ‘older’ C in subsoils under drought.

Acknowledgments We would like to thank N. Buchmann (ETH Zurich) and U. Feller (University of Bern) for initiating the drought experiment, and M.W.I. Schmidt, A. Heim (University of Zurich) and R. Siegwolf (PSI) for planning this project and discussing data. I. Woodhatch, B. Kaegi and M. Hilf provided technical assistance, and S. Gregori, N. Lang and M. Silva (all University of Zurich) helped with data collection in the field. We would also like to thank the following persons at WSL: A. Zürcher, D. Christen, P. Schleppei and O. Schramm for lab assistance and technical support; N. Hajjar for TOC analysis; B. Frey provided the litterbags; and A. Bergau has helped with modeling of water fluxes. K. Roth (University of Zurich) provided the soil data; A. Gilgen and M. J. Zeeman (ETH Zurich) provided the meteorological data. M. Saurer (PSI) supported the isotope analyses. Special thanks are granted to E. Bärtschi for logistic and financial support. The study was financially supported by the Swiss National Foundation (SNF) National Centre of Competence in Research, NCCR Climate project Plant and Soil.

References

- Arrouays D, Deslais W, Badeau V (2001) The carbon content of topsoil and its geographical distribution in France. *Soil Use Manag* 17:7–11
- Bahn M, Rodeghiero M, Anderson-Dunn M et al (2008) Soil respiration in European grasslands in relation to climate and assimilate supply. *Ecosystems* 11:1352–1367. doi: [10.1007/s10021-008-9198-0](https://doi.org/10.1007/s10021-008-9198-0)
- Bocock KL, Gilbert OJ (1957) The disappearance of leaf litter under different woodland conditions. *Plant Soil* 9:179–185
- Borken W, Matzner E (2009) Introduction: impact of extreme meteorological events on soils and plants. *Glob Change Biol* 15:781. doi: [10.1111/j.1365-2486.2009.01893.x](https://doi.org/10.1111/j.1365-2486.2009.01893.x)
- Borken W, Savage K, Davidson EA, Trumbore S (2006) Effects of experimental drought on soil respiration and radiocarbon efflux from a temperate forest soil. *Glob Change Biol* 12:177–193. doi: [10.1111/j.1365-2486.2005.01058.x](https://doi.org/10.1111/j.1365-2486.2005.01058.x)
- Bradford MA, Davies CA, Frey SD et al (2008) Thermal adaptation of soil microbial respiration to elevated temperature. *Ecol Lett* 11:1316–1327. doi: [10.1111/j.1461-0248.2008.01251.x](https://doi.org/10.1111/j.1461-0248.2008.01251.x)
- Caprez R, Niklaus PA, Koerner C (2012) Forest soil respiration reflects plant productivity across a temperature gradient in the Alps. *Oecologia* 170:1143–1154. doi: [10.1007/s00442-012-2371-3](https://doi.org/10.1007/s00442-012-2371-3)
- Chou WW, Silver WL, Jackson RD et al (2008) The sensitivity of annual grassland carbon cycling to the quantity and timing of rainfall. *Glob Change Biol* 14:1382–1394. doi: [10.1111/j.1365-2486.2008.01572.x](https://doi.org/10.1111/j.1365-2486.2008.01572.x)
- Ciais P, Reichstein M, Viovy N et al (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437:529–533. doi: [10.1038/nature03972](https://doi.org/10.1038/nature03972)
- Conant RT, Ryan MG, Agren GI et al (2011) Temperature and soil organic matter decomposition rates—synthesis of current knowledge and a way forward. *Glob Change Biol* 17:3392–3404. doi: [10.1111/j.1365-2486.2011.02496.x](https://doi.org/10.1111/j.1365-2486.2011.02496.x)
- Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440:165–173. doi: [10.1038/nature04514](https://doi.org/10.1038/nature04514)
- De Boeck HJ, Verbeeck H (2011) Drought-associated changes in climate and their relevance for ecosystem experiments and models. *Biogeosciences* 8:1121–1130. doi: [10.5194/bg-8-1121-2011](https://doi.org/10.5194/bg-8-1121-2011)
- Dilling J, Kaiser K (2002) Estimation of the hydrophobic fraction of dissolved organic matter in water samples using UV photometry. *Water Res* 36:5037–5044
- Dirks I, Navon Y, Kanas D et al (2010) Atmospheric water vapor as driver of litter decomposition in Mediterranean shrubland and grassland during rainless seasons. *Glob Change Biol* 16:2799–2812. doi: [10.1111/j.1365-2486.2010.02172.x](https://doi.org/10.1111/j.1365-2486.2010.02172.x)
- Don A, Schulze E-D (2008) Controls on fluxes and export of dissolved organic carbon in grasslands with contrasting soil types. *Biogeochemistry* 91:117–131. doi: [10.1007/s10533-008-9263-y](https://doi.org/10.1007/s10533-008-9263-y)
- Eliasson PE, McMurtrie RE, Pepper DA et al (2005) The response of heterotrophic CO₂ flux to soil warming. *Glob Change Biol* 11:167–181. doi: [10.1111/j.1365-2486.2004.00878.x](https://doi.org/10.1111/j.1365-2486.2004.00878.x)
- Eugster W, Leuenberger H (2007) *Alpine Landwirtschaft: 40 Jahre ETH-Forschung am Albulapass. Die Alpen* 83:56–59
- Eugster W, Zeeman M (2006) Micrometeorological techniques to measure ecosystem-scale greenhouse gas fluxes for model validation and improvement. In: Soliva CR, Takahashi J, Kreuzer M (eds) *Greenhouse gases and animal agriculture: an update. International Congress Series No. 1293. Elsevier, The Netherlands*, pp 66–75
- Frei C, Schoell R, Schmidli J et al (2006) Future change of precipitation extremes in Europe: intercomparison of scenarios from regional climate models. *J Geophys Res* 111:1–22. doi: [10.1029/2005JD005965](https://doi.org/10.1029/2005JD005965)
- Fröberg M, Berggren D, Hagedorn F (2007) The contribution of fresh litter to dissolved organic carbon leached from a coniferous forest floor. *Eur J Soil Sci* 58:108–114. doi: [10.1111/j.1365-2389.2006.00812.x](https://doi.org/10.1111/j.1365-2389.2006.00812.x)
- Gilgen AK, Buchmann N (2009) Response of temperate grasslands at different altitudes to simulated summer drought differed but scaled with annual precipitation. *Biogeosciences* 6:2525–2539
- Graf Pannatier E, Thimonier A, Schmitt M et al (2011) A decade of monitoring at Swiss Long-Term Forest Ecosystem Research (LWF) sites: can we observe trends in atmospheric acid deposition and in soil solution acidity? *Environ Monit Assess* 174:3–30. doi: [10.1007/s10661-010-1754-3](https://doi.org/10.1007/s10661-010-1754-3)
- Hagedorn F, Saurer M, Blaser P (2004) A ¹³C tracer study to identify the origin of dissolved organic carbon in forested mineral soils. *Eur J Soil Sci* 55:91–100. doi: [10.1046/j.1365-2389.2003.00578.x](https://doi.org/10.1046/j.1365-2389.2003.00578.x)
- Harper CW, Blair JM, Fay PA et al (2005) Increased rainfall variability and reduced rainfall amount decreases soil CO₂ flux in a grassland ecosystem. *Glob Change Biol* 11:322–334. doi: [10.1111/j.1365-2486.2005.00899.x](https://doi.org/10.1111/j.1365-2486.2005.00899.x)
- Hebeisen T, Luescher A, Noesberger J (1997) Effects of elevated atmospheric CO₂ and nitrogen fertilisation on yield of *Trifolium repens* and *Lolium perenne*. *Acta Oecol Int J Ecol* 18:277–284
- Hentschel K, Borken W, Matzner E (2007) Leaching losses of inorganic N and DOC following repeated drying and wetting of a spruce forest soil. *Plant Soil* 300:21–34. doi: [10.1007/s11104-007-9385-3](https://doi.org/10.1007/s11104-007-9385-3)
- Hiller R, Zeeman M, Eugster W (2008) Eddy-covariance flux measurements in the complex terrain of an Alpine valley in Switzerland. *Bound-Layer Meteorol* 127:449–467. doi: [10.1007/s10546-008-9267-0](https://doi.org/10.1007/s10546-008-9267-0)
- Houghton RA (2007) Balancing the global carbon budget. *Annu Rev Earth Planet Sci* 35:313–347. doi: [10.1146/annurev.earth.35.031306.140057](https://doi.org/10.1146/annurev.earth.35.031306.140057)
- Jansson P-E, Karlberg L (2004) Coupled heat and mass transfer model for soil-plant atmosphere systems. Department of Civil and Environmental Engineering, Royal Institute of Technology, Stockholm
- Jentsch A (2006) Extreme climatic events in ecological research. *Front Ecol Environ* 5:235–236
- Joos O, Saurer M, Heim A et al (2008) Can we use the CO₂ concentrations determined by continuous-flow isotope ratio mass spectrometry-try from small samples for the Keeling plot approach? *Rapid Commun Mass Spec* 22:4029–4034. doi: [10.1002/rcm.3827](https://doi.org/10.1002/rcm.3827)
- Joos O, Hagedorn F, Heim A et al (2010) Summer drought reduces total and litter-derived soil CO₂ effluxes in

- temperate grassland—clues from a ^{13}C litter addition experiment. *Biogeosciences* 7:1031–1041
- Kaiser K, Guggenberger G (2000) The role of DOM sorption to mineral surfaces in the preservation of organic matter in soils. *Org Geochem* 31:711–725
- Kaiser K, Kalbitz K (2012) Cycling downwards—dissolved organic matter in soils. *Soil Biol Biochem* 52:29–32. doi:[10.1016/j.soilbio.2012.04.002](https://doi.org/10.1016/j.soilbio.2012.04.002)
- Kalbitz K, Solinger S, Park JH et al (2000) Controls on the dynamics of dissolved organic matter in soils: a review. *Soil Sci* 165:277–304
- Kalbitz K, Schmerwitz J, Schwesig D, Matzner E (2003) Biodegradation of soil-derived dissolved organic matter as related to its properties. *Geoderma* 113:273–291. doi:[10.1016/S0016-7061\(02\)00365-8](https://doi.org/10.1016/S0016-7061(02)00365-8)
- Kindler R, Siemens J, Kaiser K et al (2010) Dissolved carbon leaching is a crucial component of the net ecosystem carbon balance. *Glob Change Biol* 17:1167–1185. doi:[10.1111/j.1365-2486.2010.02282.x](https://doi.org/10.1111/j.1365-2486.2010.02282.x)
- Knapp AK, Smith MD (2001) Interannual variability in net primary production and precipitation—response. *Science* 293:U2. doi:[10.1126/science.293.5536.1723a](https://doi.org/10.1126/science.293.5536.1723a)
- Knapp AK, Fay PA, Blair JM et al (2002) Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* 298:2202–2205. doi:[10.1126/science.1076347](https://doi.org/10.1126/science.1076347)
- Kreyling J, Beierkuhnlein C, Elmer M et al (2008) Soil biotic processes remain remarkably stable after 100-year extreme weather events in experimental grassland and heath. *Plant Soil* 308:175–188. doi:[10.1007/s11104-008-9617-1](https://doi.org/10.1007/s11104-008-9617-1)
- Lal R (2004) Soil carbon sequestration to mitigate climate change. *Geoderma* 123:1–22. doi:[10.1016/j.geoderma.2004.01.032](https://doi.org/10.1016/j.geoderma.2004.01.032)
- Leifeld J, Bassin S, Fuhrer J (2005) Carbon stocks in Swiss agricultural soils predicted by land-use, soil characteristics, and altitude. *Agric Ecosyst Environ* 105:255–266. doi:[10.1016/j.agee.2004.03.006](https://doi.org/10.1016/j.agee.2004.03.006)
- Leifeld J, Zimmermann M, Fuhrer J, Conen Z (2009) Storage and turnover of carbon in grassland soils along an elevation gradient in the Swiss Alps. *Glob Change Biol* 15:668–679. doi:[10.1111/j.1365-2486.2008.01782.x](https://doi.org/10.1111/j.1365-2486.2008.01782.x)
- Lieth H (1975) Modeling the primary productivity of the world. In: *Primary productivity of the biosphere*. Springer, Berlin
- Loranger G, Ponge JF, Imbert D, Lavelle P (2002) Leaf decomposition in two semi-evergreen tropical forests: influence of litter quality. *Biol Fertil Soils* 35:247–252. doi:[10.1007/s00374-002-0467-3](https://doi.org/10.1007/s00374-002-0467-3)
- Luterbacher J, Dietrich D, Xoplaki E et al (2004) European seasonal and annual temperature variability, trends, and extremes since 1500. *Science* 303:1499–1503
- Manzoni S, Schimel JP, Porporato A (2012) Responses of soil microbial communities to water stress: results from a meta-analysis. *Ecology* 93:930–938
- Meehl GA, Karl T, Easterling DR et al (2000) An introduction to trends in extreme weather and climate events: observations, socioeconomic impacts, terrestrial ecological impacts, and model projections. *Bull Am Meteorol Soc* 81:413–416
- Meehl GA, Stocker TF, Collins WD et al (2007) Global climate projections. In: Solomon S, Qin D, Manning M et al (eds) *Climate change 2007: the physical science basis*. Contribution of Working Group I to the Fourth Assessment Report of the Inter-governmental Panel on Climate Change. Cambridge University Press, Cambridge, pp 747–846
- Muhr J, Borken W (2009) Delayed recovery of soil respiration after wetting of dry soil further reduces C losses from a Norway spruce forest soil. *J Geophys Res* 114:G04023. doi:[10.1029/2009JG000998](https://doi.org/10.1029/2009JG000998)
- Muhr J, Franke J, Borken W (2010) Drying–rewetting events reduce C and N losses from a Norway spruce forest floor. *Soil Biol Biochem* 42:1303–1312. doi:[10.1016/j.soilbio.2010.03.024](https://doi.org/10.1016/j.soilbio.2010.03.024)
- Müller M, Alewell C, Hagedorn F (2009) Effective retention of litter-derived dissolved organic carbon in organic layers. *Soil Biol Biochem* 41:1066–1074. doi:[10.1016/j.soilbio.2009.02.007](https://doi.org/10.1016/j.soilbio.2009.02.007)
- R Development Core and Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Raich JW, Schlesinger WH (1992) The global carbon-dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus B* 44:81–99
- Rebetez M, Mayer H, Dupont O, Schindler D, Gartner, Kropp JP, Menzel A (2006) Heat and drought 2003 in Europe: a climate synthesis. *Ann For Sci* 63:569–577
- Risch AC, Jurgensen MF, Frank DA (2007) Effects of grazing and soil micro-climate on decomposition rates in a spatio-temporally heterogeneous grassland. *Plant Soil* 298:191–201. doi:[10.1007/s11104-007-9354-x](https://doi.org/10.1007/s11104-007-9354-x)
- Roth K (2006) *Bodenkartierung und GIS-basierte Kohlenstoffinventur von Graslandböden: Untersuchungen an den ETH Forschungsstationen Chamau und Frübüel (ZG, Schweiz)*. Diploma Thesis, University of Zurich, Switzerland, 132 pp
- Ruehr NK, Offermann CA, Gessler A et al (2009) Drought effects on allocation of recent carbon: from beech leaves to soil CO₂ efflux. *New Phytol* 184:950–961. doi:[10.1111/j.1469-8137.2009.03044.x](https://doi.org/10.1111/j.1469-8137.2009.03044.x)
- Sanaullah M, Chabbi A, Rumpel C, Kuzyakov Y (2012) Carbon allocation in grassland communities under drought stress followed by ^{14}C pulse labeling. *Soil Biol Biochem* 55:132–139. doi:[10.1016/j.soilbio.2012.06.004](https://doi.org/10.1016/j.soilbio.2012.06.004)
- Sanderman J, Amundson R (2008) A comparative study of dissolved organic carbon transport and stabilization in California forest and grassland soils. *Biogeochemistry* 89:309–327. doi:[10.1007/s10533-008-9221-8](https://doi.org/10.1007/s10533-008-9221-8)
- Schärer M (2003) *Kurzbericht der Fallstudie Alp Weissenstein. Nährstoffanalysen in Alpweiden*. Sommer 2002, Term Paper, ETH Zurich, Switzerland, 44 pp
- Schimel JP, Balsler TC, Wallenstein M (2007) Microbial stress-response physiology and its implications for ecosystem function. *Ecology* 88:1386–1394. doi:[10.1890/06-0219](https://doi.org/10.1890/06-0219)
- Schindlbacher A, Wunderlich S, Borken W et al (2012) Soil respiration under climate change: prolonged summer drought offsets soil warming effects. *Glob Change Biol* 18:2270–2279. doi:[10.1111/j.1365-2486.2012.02696.x](https://doi.org/10.1111/j.1365-2486.2012.02696.x)
- Schwalm CR, Williams CA, Schaefer K et al (2012) Reduction in carbon uptake during turn of the century drought in western North America. *Nat Geosci* 5:551–556. doi:[10.1038/NNGEO1529](https://doi.org/10.1038/NNGEO1529)
- Scott RL, Jenerette D, Potts DL, Huxman TE (2009) Effects of seasonal drought on net carbon dioxide exchange from a

- woody-plant-encroached semiarid grassland. *J Geophys Res* 114:G04004. doi:[10.1029/2008JG000900](https://doi.org/10.1029/2008JG000900)
- Siemens J (2003) The European carbon budget: a gap. *Science* 302:1681
- Weltzin JF, Loik ME, Schwinning S et al (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience* 53:941–952
- White A, Cannell MGR, Friend AD (2000) The high-latitude terrestrial carbon sink: a model analysis. *Glob Change Biol* 6:227–245
- Zeeman MJ (2008) Environmental processes affecting the carbon dioxide budget of grasslands along an elevational gradient in Switzerland. Dissertation, ETH Zurich
- Zeeman MJ, Hiller R, Gilgen AK et al (2010) Management and climate impacts on net CO₂ fluxes and carbon budgets of three grasslands along an elevational gradient in Switzerland. *Agric For Meteorol* 150:519–530. doi:[10.1016/j.agrformet.2010.01.011](https://doi.org/10.1016/j.agrformet.2010.01.011)
- Zimmermann M, Meir P, Bird MI et al (2009) Climate dependence of heterotrophic soil respiration from a soil-translocation experiment along a 3000 m tropical forest altitudinal gradient. *Eur J Soil Sci* 60:895–906. doi:[10.1111/j.1365-2389.2009.01175.x](https://doi.org/10.1111/j.1365-2389.2009.01175.x)