Biogeosciences, 11, 961–975, 2014
www.biogeosciences.net/11/961/2014/
doi:10.5194/bg-11-961-2014

Biogeosciences Open Access

The impact of extreme summer drought on the short-term carbon coupling of photosynthesis to soil CO_2 efflux in a temperate grassland

S. Burri[1], P. Sturm[1,*], U. E. Prechsl[1], A. Knohl[2], and N. Buchmann[1]

[1]Institute of Agricultural Sciences, ETH Zurich, Zurich, Switzerland
[2] Büsgen-Institute, Chair of Bioclimatology, Georg-August-University Göttingen, Göttingen, Germany
[*]now at: Tofwerk AG, Thun, Switzerland

Correspondence to: S. Burri (susanne.burri@usys.ethz.ch)

Received: 7 June 2013 – Published in Biogeosciences Discuss.: 11 July 2013
Revised: 30 December 2013 – Accepted: 3 January 2014 – Published: 20 February 2014

Abstract. Along with predicted climate change, increased risks for summer drought are projected for Central Europe. However, large knowledge gaps exist in terms of how drought events influence the short-term ecosystem carbon cycle. Here, we present results from $^{13}CO_2$ pulse labeling experiments at an intensively managed lowland grassland in Switzerland. We investigated the effect of extreme summer drought on the short-term coupling of freshly assimilated photosynthates in shoots to roots as well as to soil CO_2 efflux.

Summer drought was simulated using rainout shelters during two field seasons (2010 and 2011). Soil CO_2 efflux and its isotopic composition were measured with custom-built chambers coupled to a quantum cascade laser spectrometer (QCLAS-ISO, Aerodyne Research Inc., MA, USA). During the 90 min pulse labeling experiments, we added 99.9 atom % $^{13}CO_2$ to the grass sward. In addition to the isotopic analysis of soil CO_2 efflux, this label was traced over 31 days into bulk shoots, roots and soil.

Drought reduced the incorporation of recently fixed carbon into the shoots, but increased the relative allocation of fresh assimilates below ground compared to the control grasslands. Contrary to our hypothesis, we did not find a change of allocation speed in response to drought. Although drought clearly reduced soil CO_2 efflux rates, about 75 % of total tracer uptake in control plots was lost via soil CO_2 efflux during 19 days after pulse labeling, compared to only about 60 % under drought conditions. Thus, the short-term coupling of above- and below-ground processes was reduced in response to summer drought. The occurrence of a natural spring drought in 2011 lead to comparable albeit weaker drought responses increasing the confidence in the generalizability of our findings.

1 Introduction

Models of future climate not only project changes in mean climate, but also changes in occurrence and characteristics of extreme events, thus in climate variability (Seneviratne et al., 2012). Drought events have recently gained importance in the discussion on climatic change and the need for adaption (IPCC, 2012), since precipitation patterns are expected to change in the future. For Central Europe, regional climate scenarios project a likely reduction of summer mean precipitation and an increased risk of summer drought (Christensen et al., 2007). For Switzerland, mean summer precipitation is projected to decrease by 18–24 % in 2085 (considering the medium estimates of the IPCC A1B emission scenario), along with an increased risk of drought (CH2011, 2011). But its impact on terrestrial ecosystems is still unclear.

Plant responses to changing climate variability, specifically, to drought, are not well understood and are insufficiently represented in global carbon models (Reyer et al., 2013; van der Molen et al., 2011), making the projection of future drought effects on carbon cycling difficult. This is why Ostle et al. (2009) suggested that in order to improve climate change predictions and carbon cycle modelling, plant–soil

interactions should be better represented in global carbon models. Especially the complex coupling of above- and below-ground processes (Kuzyakov and Gavrichkova, 2010), i.e. mechanisms, speed and potential time lags of carbon assimilation, allocation below ground and finally the release to the atmosphere by soil CO_2 efflux, still bears many uncertainties (Brüggemann et al., 2011; Epron et al., 2012). Moreover, the influence of environmental stresses as for example drought on such processes is not resolved yet (Brüggemann et al., 2011).

The remarkable heat wave and drought event in Central Europe in 2003 caused a Europe-wide reduction in gross primary productivity (Ciais et al., 2005). However, this study consisted mainly of forest sites, while grasslands were only represented by one site. But grasslands are widespread in Europe and changes in precipitation patterns potentially have large effects on grassland management and agriculture in general (Hopkins and Del Prado, 2007). On the other hand, grasslands have been shown to respond differently to heatwaves than forests: in contrast to forests, grasslands increase evaporation at higher solar radiation and temperature, not altering their water use efficiency (WUE), which ultimately leads to soil moisture depletion (Teuling et al., 2010; Wolf et al., 2013) and wilting/death of vegetation. Thus, it is likely that grasslands also have different responses to drought in terms of short-term carbon cycling and below-ground carbon allocation compared to forests. While several studies addressed the effect of clipping or shading on carbon allocation and found photosynthesis to be an immediate source for soil CO_2 efflux (Craine et al., 1998; Wan and Luo, 2003; Bahn et al., 2009), none of them has investigated the impact of drought under field conditions so far. Drought-effects on below-ground carbon allocation of grasses have only been studied under laboratory conditions (Sanaullah et al., 2012; Huang and Fu, 2000), where a proportionally higher allocation to roots in response to drought had been found. If drought effects in the field show the same patterns as under controlled laboratory conditions or are similar to effects of clipping or shading remains to be shown.

Thus, we tested the effects of increased summer drought on grassland ecosystems in a Swiss ecosystem manipulation experiment. Several aspects of drought stress had been investigated in recent years, like the effect on community productivity (Gilgen and Buchmann, 2009), species composition (Gilgen et al., 2010), plant ecophysiology (Signarbieux and Feller, 2011) or litter decomposition (Joos et al., 2010). In the current study, we present results from $^{13}CO_2$ pulse labeling experiments performed in summer 2010 and summer 2011 within the same experiment at an intensively managed, lowland grassland site in Switzerland. The experiment aimed at studying the short-term carbon dynamics and the coupling of photosynthesis and soil CO_2 efflux in response to a simulated extreme summer drought. Continuous measurements by quantum cascade laser spectroscopy enabled high temporal resolution measurements of soil CO_2 efflux and its isotopic composition. Combined with isotopic analyses of above- and below-ground biomass, we could trace freshly assimilated carbon from photosynthesis to soil CO_2 efflux.

We hypothesized a tight coupling between above- and below-ground systems under normal conditions, but expected the coupling to be reduced under drought stress. Which of the two alternative explanations, (1) a higher residence time of fresh assimilates in the above-ground biomass as observed for beech saplings under drought (Ruehr et al., 2009) or (2) a higher relative below-ground allocation of recent assimilates as had been shown under laboratory conditions (Sanaullah et al., 2012 for grasses, Barthel et al., 2011a for beech saplings) is responsible for such a reduced coupling remains to be investigated. Independent of the exact distribution within the plant, we anticipated the use of fresh assimilates in soil CO_2 efflux to be reduced under drought conditions (Ruehr et al., 2009; Barthel et al., 2011a).

2 Methods

2.1 Experimental set-up

Experiments were conducted at a grassland in the Swiss lowlands, at Chamau, Switzerland (47°12′37″ N, 8°24′38″ E; 393 m a.s.l). The grassland is intensively managed, with up to six cuts per year, and regularly fertilized. It thus represents the widespread agricultural use of Swiss lowlands grasslands which is optimized for high fodder production. The original seed mixture (applied in 2002) consisted of smooth meadowgrass (*Poa pratensis*), English ryegrass *(Lolium perenne)* and white clover *(Trifolium repens)*, however, up to 20 species were found on the experimental plots (Gilgen et al., 2010). The mean annual precipitation sum at Chamau is 1151 mm and the mean annual temperature is 9.1 °C (Finger et al., 2013). The soil type was classified as a Cambisol (Roth, 2006).

Summer drought was simulated by means of rainout shelters which had been installed for extended periods of time and used for experiments at this site since 2005. The plots used for this study were newly established in 2009, because the ones used since 2005 at the same site were heavily damaged by mice infestation. The experimental set-up was organized in a block design with six blocks. Each block consisted of a control (ctrl) and a drought-treated plot (tmt) which was covered by shelters (3 m × 3.5 m) during the treatment period. The core plots had a dimension of 1 m × 2 m and were managed according to the management of the surrounding grassland, however, no fertilizer was applied. Three of the six experimental blocks were equipped with sensors for continuously measuring microclimate on control and treatment plots. At 5, 15 and 30 cm depth, soil temperature (Precision IC Temperature Transducer AD592AN, Analog Devices, Norwood, MA, USA) and soil moisture

(ECH_2O EC-5, Decagon Devices, Inc. Pullman, WA, USA) were measured. At 180 cm, photosynthetically active radiation (PAR) was recorded (PAR LITE, Kipp & Zonen B. V., Delft, Netherlands). On two of the three blocks used for measuring microclimate, air temperature was recorded at 160 cm (ventilated system with the same sensors as for soil temperature records), and relative humidity of air was measured at 60 cm on one of the three blocks (HC2-S3C05, Rotronic, Bassersdorf, Switzerland). Data were logged every 10 min with data loggers (Campbell Scientific Inc., Logan, UT, USA). Close to the experimental plots, a permanent eddy-covariance station was located where precipitation was recorded.

We simulated summer drought for 8–12 weeks during the summer months with rainout shelters (Table 1), which had an area of 3 m × 3.5 m, similar in design to Kahmen et al. (2005). The shelters were tunnel shaped, 2.3 m in height and covered with UV-B penetrable, transparent plastic foils (UV B-window, folitec, Westerburg, DE). Two sides of the shelters were open to ensure sufficient air circulation. The core plot area was centered underneath the shelters to avoid edge effects. The effect of the shelter on air and soil temperatures was minor and is described in detail in Gilgen and Buchmann (2009).

2.2 $^{13}CO_2$ pulse labeling

Pulse labeling experiments were performed on 19, 20, and 21 July 2010 as well as on 7, 9 and 10 June 2011. In each year, three experimental blocks (each consisting of a control and a treatment plot) were labeled, with one block being labeled per day, starting at around 09:30 CET and lasting for 90 min. During pulse labeling, transparent labeling chambers (plexiglas, 1 m × 1 m × 0.7 m), covering 1 m^2 of grass sward and built after the design in Bahn et al. (2009), were placed on metal frames, reaching around 10 cm into the soil. Pulse labeling was achieved by adding 99.9 atom % $^{13}CO_2$ (Cambridge Isotope Laboratories, Inc. (CIL), Andover, MA, USA) during 90 min to the experimental plots. Cooling of the labeling chambers was done by ventilation fans and commercial ice packs. Control and treatment plots were labeled in parallel, in order to guarantee pulse labeling of one experimental block under identical environmental conditions. CO_2 concentrations as well as the isotopic composition of the air inside the labeling chambers were monitored by two infrared gas analyzers (Li840 and Li6262; Li-Cor Biosciences Inc., Lincoln, NE, USA) that had previously been tested for their $^{13}CO_2$ sensitivities (Barthel et al., 2011b). As conditions inside only one labeling chamber could be monitored at a time, we regularly switched between the two labeling chambers (one labeling a control plot, the other labeling a treatment plot). We labeled one chamber headspace up to 600 ppm, then switched measurements to the second labeling chamber, which was labeled as well up to 600 ppm. In the meantime, concentrations in the first chamber decreased due to photosynthetic uptake. Thus, monitoring was switched back to the first chamber, and a new labeling pulse was given. During the 90 min of labeling, we switched between the two chambers about every 5–10 min, keeping CO_2 concentrations inside both labeling chambers relatively constant at around 400–600 ppm. This increase above ambient conditions was necessary to assure sufficient tracer uptake to address our objectives.

2.3 Sampling procedure

Right after the 90 min of pulse labeling, we started a very intensive sampling campaign, during the first days after labeling, which was continued on a weekly schedule until around 30 days after pulse labeling. The sampling pattern in 2010 slightly differed from that in 2011, as the sampling scheme was intensified in 2011. In 2010, samples were taken 0, 2, 6, 10, 22, 48 h and 4 days (intensive campaign) as well as about 10, 17, 24, 31 days after pulse labeling. As the four last samples were all taken at the same day for the three experimental blocks, the time difference in days after pulse labeling differed slightly among the three replicates. In 2011, samples were taken 0, 2, 6, 10, 24, 34, 48 h and 4 days after pulse labeling as well as about 10, 17, 26, 31, 81 and 125 days after pulse labeling. Again, the last (six) samples were all taken on the same day for the three blocks. Samples at about 81 and 125 days after pulse labeling were taken before the grassland was cut.

First, shoots were cut at ground level, using a small metal frame (with an area of 5 × 7 cm), and kept cool on ice until microwave treatment (see below). Then, a soil sample was taken with a soil core auger down to 15 cm depth (with an inner diameter of 5.5 cm) at the place where the shoots had been harvested. The soil was sieved with a 2 mm mesh, resulting in a root sample and a root-free soil sample that was frozen and later freeze-dried. Thereafter, the roots were carefully washed with a 0.4 mm mesh. Shortly after sampling, shoots and roots were put into a microwave in order to stop all biochemical processes, before being dried at 60 °C in the drying oven. All samples were weighed, ground and subsequently analyzed by isotope ratio mass spectrometry for $\delta^{13}C$ and C content.

2.4 Measurements of soil CO_2 efflux by laser spectroscopy

In order to trace carbon in soil CO_2 efflux, soil CO_2 efflux and its isotopic composition was measured by quantum cascade laser spectroscopy (QCLAS-ISO, Aerodyne Research Inc., MA, USA) on three blocks in July–August 2010 (17 July–19 August) and June 2011 (1–30 June), thus, before, during and after the pulse labeling experiments. Shallow PVC collars (with an inner diameter of 103 mm, reaching around 1–2 cm into the soil) were installed in early spring at each plot, the vegetation growing inside the collars

Table 1. Overview of shelter duration and excluded precipitation in 2010 and 2011 (in brackets percentage of annual rainfall) as well as soil water content (SWC) at 5 cm, 15 cm and 30 cm depth under control (ctrl) and treatment (tmt) conditions (mean ± SD).

Year			2010	2011
Shelter duration			20 May–11 August	5 May–1 July
Number of days			83	57
Excluded precipitation [mm]			440 (39 %)	231 (21 %)
Annual precipitation [mm]			1139	1084
SWC [Vol %]	5 cm	ctrl	29.8 ± 7.9	26.0 ± 4.2
		tmt	15.1 ± 8.5	17.0 ± 1.7
		tmt/ctrl [%]	51	65
	15 cm	ctrl	33.5 ± 5.9	26.3 ± 4.0
		tmt	22.5 ± 7.9	18.1 ± 2.0
		tmt/ctrl [%]	67	69
	30 cm	ctrl	41.1 ± 2.2	35.5 ± 3.3
		tmt	38.9 ± 3.9	29.2 ± 1.9
		tmt/ctrl [%]	95	82

was clipped on a regular basis. Steady-state-flow-through soil efflux chambers, resembling those of Rayment and Jarvis (1997), were custom-made and could be fixed to the collars, installed permanently in the field. Air was pumped at a continuous flow rate (2010: 0.472 ± 0.005 L min^{-1}; 2011: 0.536 ± 0.002 L min^{-1}; mean ± SD) from the soil chambers to the laser spectrometer, which was installed in a dedicated shed with air conditioning nearby. While one chamber was measured, the flow rate in the other chambers was maintained by an additional purge pump to guarantee steady-state conditions. Switching between the chambers was achieved by a valve box steered by a custom-written LabVIEW program. With this set-up, it was possible to calculate soil CO_2 efflux (F) as well as its isotopic composition continuously as follows:

$$F = \frac{f \cdot (c_{\text{out}} - c_{\text{in}})}{A}, \quad (1)$$

where f is the flow rate through the soil CO_2 efflux chambers (mol s^{-1}), c_{out} (µmol mol^{-1}) the CO_2 concentration inside the soil CO_2 efflux chambers, c_{in} (µmol mol^{-1}) the CO_2 concentration of outside air, and A the ground area of the soil CO_2 efflux chambers (m^2). The ^{13}C concentration of soil CO_2 efflux was calculated based on an isotopic mass balance approach, resulting in the respective δ^{13}C values ($\delta^{13}C_F$):

$$\delta^{13}C_F = \frac{\delta^{13}C_{\text{out}} \cdot c_{\text{out}} - \delta^{13}C_{\text{in}} \cdot c_{\text{in}}}{c_{\text{out}} - c_{\text{in}}}, \quad (2)$$

where

$$\delta^{13}C = \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \quad (3)$$

and R stands for the $^{13}C : {}^{12}C$ isotope ratio of the sample and the international V-PDB standard (0.0111802), respectively.

At each labeled plot, one soil CO_2 efflux chamber was installed, which was measured at least hourly over the entire measurements periods (about one month in both years), but more frequently in the first hours after pulse labeling. This enabled us to measure the tracer release with soil CO_2 efflux. The laser spectrometer was calibrated every hour by a two-point calibration (with two calibration gases of known isotopic composition) and a linearity calibration, where another calibration gas was dynamically diluted with CO_2-free air. In order to check for long-term stability, a control standard was measured after each calibration. The estimated uncertainty for δ^{13}C was ca. 0.33 ‰ in 2010 and ca. 0.21 ‰ in 2011. For more detailed information on calibration issues refer to Nelson et al. (2008) and Sturm et al. (2012).

In order to estimate the error of the measurements, the error (standard deviation) of each of the measured factors in Eqs. (1) and (2) was propagated by Gaussian error propagation into an overall error of the soil CO_2 efflux and of its isotopic composition. Thereafter, a filtering was applied, discarding values with propagated errors for CO_2 efflux > 0.9 µmol m^{-2} s^{-1} (according to the 95th percentile of the propagated error for control chambers in 2011) and values with propagated errors for the δ^{13}C of soil CO_2 efflux > 35 ‰ (according to the 80th percentile of the propagated error of the treatment chambers in 2011). The resulting overall data availability in 2010 was 79 % and 80 % for control and treatment chambers, respectively, and 72 % for control and 66 % for treatment chambers in 2011.

2.5 Calculation of ^{13}C excess in above- and below-ground biomass and soil CO_2 efflux

In order to express the amount of ^{13}C label found in above- and below-ground biomass above the natural isotopic background, the ^{13}C enrichment or the excess atom fraction

($x^E(^{13}C)_{plant/reference}$) was calculated as follows (note: we use the nomenclature after Coplen, 2011, where for example the term "atom percent excess" is deprecated):

$$x^E(^{13}C)_{plant/pre\text{-}lab} = x(^{13}C)_{plant} - x(^{13}C)_{plant(pre\text{-}lab)}, \quad (4)$$

where $x(^{13}C)_{plant}$ refers to the atom fraction of the respective labeled plant sample and $x(^{13}C)_{plant\,(pre\text{-}lab)}$ to the atom fraction of plant samples taken before pulse labeling (in our case: 2011). The atom fraction of the respective plant sample is defined as

$$x(^{13}C)_{plant} = \frac{n(^{13}C)_{plant}}{n(^{13}C)_{plant} + n(^{12}C)_{plant}}, \quad (5)$$

where $n(^iC)_{plant}$ is the amount of isotope ^iC per plant part. As this amount cannot directly be determined, $x(^{13}C)_{plant}$ is calculated based on the measured isotope ratio:

$$x(^{13}C)_{plant} = \frac{1}{1 + \frac{1}{(\delta^{13}C_{plant}+1)\cdot R(^{13}C/^{12}C)_{reference}}}, \quad (6)$$

where the $R(^{13}C/^{12}C)_{reference}$ is the $^{13}C:^{12}C$ isotope ratio of the international V-PDB standard. $\delta^{13}C_{plant}$ stands for the measured isotope ratio of a plant sample (Eq. 3).

In a next step, the ^{13}C excess was calculated at the community (sward) level, taking biomass pools into account (similar to Ruehr et al., 2009):

$$\text{excess}^{13}C_{plant} = \left(x(^{13}C)_{plant} - x(^{13}C)_{plant(pre\text{-}lab)}\right) \cdot DW_{plant} \cdot C_{plant}. \quad (7)$$

$\text{excess}^{13}C_{plant}$ [mg $^{13}C\,m^{-2}$] is the amount of ^{13}C found in the respective pool of above- or below-ground standing biomass. DW_{plant} refers to the standing biomass per square metre [g m^{-2}] and C_{plant} to the carbon content of the respective sample [%]. We calculated ^{13}C excess only for the first four days after pulse labeling, assuming above- and below-ground biomass pools to be relatively constant during these four days.

Since we could not destructively harvest above- and below-ground biomass at the same high temporal resolution as the soil CO_2 efflux measurements, we estimated community biomass based on anchor point measurements. Community above-ground biomass at the time of pulse labeling was estimated by a linear interpolation between the day of the last cut before pulse labeling (biomass set to zero) and the above-ground biomass measured (using sampling frames of 20×50 cm in size) with the first cut after pulse labeling.

In 2010, the interpolation was carried out for 22 July 2010, based on the cutting dates 1 July 2010 and 25 August 2010. For 2011, the interpolation was done for 10 June 2011, between the cutting dates 26 May 2011 and 15 July 2011.

Similarly, to determine standing below-ground biomass, we first averaged the root masses per replicate (only on days when all three plots had been sampled, thus $n = 3$ was available). Then, the linear interpolation was performed in the same way as described above: for 22 July 2010 between 21 July 2010 and 30 July 2010, and for 10 June 2011 between 06 June 2011 and 11 June 2011.

The amount of ^{13}C label found in soil CO_2 efflux [mg $^{13}C\,m^{-2}\,s^{-1}$] beyond natural abundance values was determined as follows:

$$\text{excess}^{13}C_F = \left(x(^{13}C)_F - x(^{13}C)_{F(pre\text{-}lab)}\right) \cdot F, \quad (8)$$

where $x(^{13}C)_F$ refers to the atom fraction of the measured soil CO_2 efflux. For $x(^{13}C)_{F(pre\text{-}lab)}$, a $\delta^{13}C$ value of -27 ‰ was assumed which corresponds to an average measured value during the pre-labeling periods.

In order to obtain the cumulative $\text{excess}^{13}C_F$ until the end of the 1-month measurement period, gaps in $\text{excess}^{13}C_F$ were linearly interpolated, $\text{excess}^{13}C_F$ aggregated to hourly values and finally summed up. The first 8 h after labeling were excluded from the cumulative consideration as they were strongly influenced by physical back diffusion of the tracer signal out of the soil (Barthel et al., 2011b). Thus, the results for the biological ^{13}C flux might be slightly underestimated by the exclusion of the first 8 h after pulse labeling. The cumulative ^{13}C excess in soil CO_2 efflux was calculated until 19 days after pulse labeling (representing to the longest possible period until measurements ended in 2011). This final analysis is based on three drought plots and one control plot in 2010 (two control plots had to be excluded due to heavy destruction by mice), and on two control plots and two treatment plots in 2011.

Last, the recovery of ^{13}C in roots and in soil CO_2 efflux was estimated in relation to the initial ^{13}C excess (0 h after labeling) found in shoots. The recovery in roots and soil CO_2 efflux was calculated as follows:

$$\text{Recovery}_{roots} = \frac{\text{excess}^{13}C_{roots}}{\text{excess}^{13}C_{shoots,t0}} \quad (9)$$

$$\text{Recovery}_F = \frac{\text{excess}^{13}C_F}{\text{excess}^{13}C_{shoots,t0}}. \quad (10)$$

While recovery in roots was calculated based on the individual replicates available per plot and then averaged per treatment, recovery in soil CO_2 efflux was calculated based on mean values per treatment to account for the lower number of replicates compared to that of the roots samples and for the spatial representation of efflux measurements.

3 Results

3.1 Meteorological conditions and drought treatment

In 2010, the pulse labeling experiments were conducted during three typical midsummer days when PAR reached

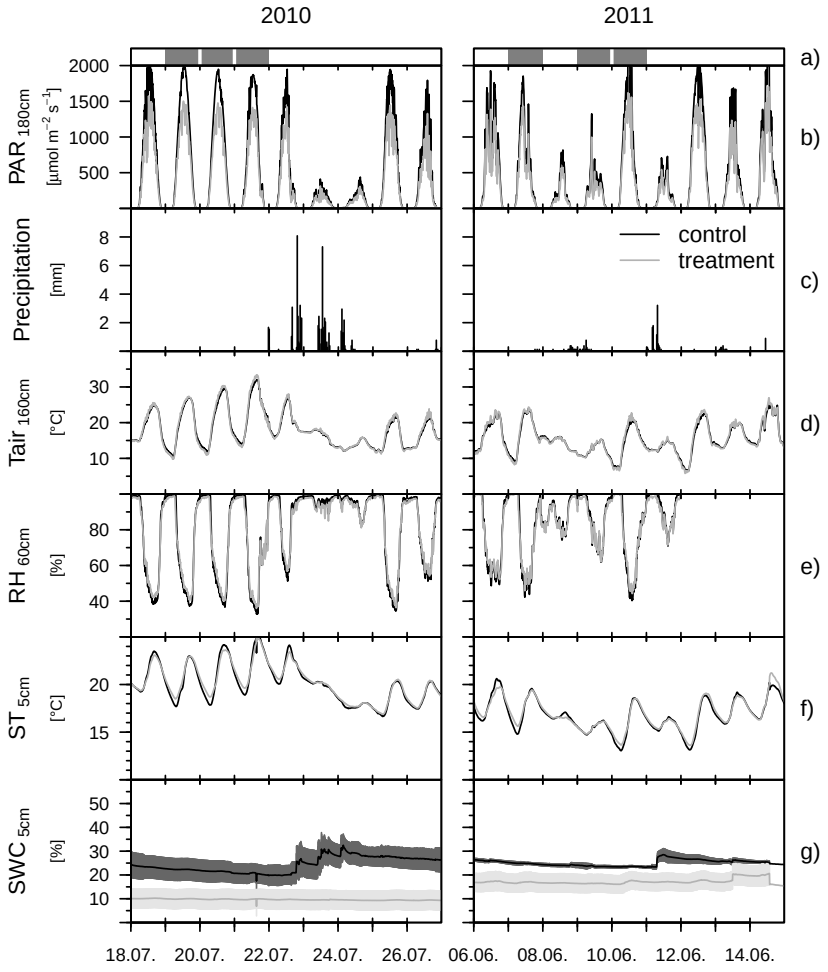

Fig. 1. Meteorological conditions during and shortly after pulse labeling experiments in 2010 (left) and 2011 (right) under control (black) and treatment (grey) conditions. **(a)** Grey shadings mark days of pulse labeling experiments, **(b)** Photosynthetically active radiation (PAR) at 180 cm height (mean, $n = 2$), **(c)** Precipitation measured at the nearby eddy-covariance station, **(d)** Air temperature (T_{air}) at 160 cm height (mean, $n = 2$), **(e)** Relative humidity (RH) above the grass sward at 60 cm height ($n = 1$), **(f)** Soil temperature at 5 cm depth (mean, $n = 3$), **(g)** Soil water content (SWC) at 5 cm depth (mean $\pm$ SE, $n = 3$).

almost 2000 µmol m^{-2} s^{-1}. Consequently, air temperatures were very high, with maxima around 30 °C, and soil temperatures higher than 25 °C. In 2011, the meteorological conditions were less stable during the pulse labeling experiments. Nevertheless, during two of the three experimental days, the conditions during the whole 90 min of pulse labeling were comparable to 2010. Overall, daily maxima of air and soil temperatures were lower in 2011 compared to 2010 (Fig. 1).

The duration of the drought treatment was shorter in 2011 compared to 2010 (Table 1), since spring 2011 was naturally already very dry (MeteoSwiss, 2012), and a "killing" experiment was to be avoided. This natural spring drought can be seen in the steadily decreasing soil moisture values at 5, 15 and 30 cm depth in April 2011 (Fig. 2). Nevertheless, we succeeded to impose a summer drought on our treatment plots. Average soil moisture was reduced in all depths in both years due to the shelters (around 30–50 % at 5 and 15 cm depth and 5–20 % at 30 cm depth; Table 1). Only during one very heavy precipitation event in June 2010, a short rise in soil moisture levels occurred, but soil moisture values dropped to the significantly lower previous levels and stayed lower during the shelter period. In general, average absolute remaining soil moisture contents at 5 and 15 cm depth were comparable in 2010 and 2011 both under control and drought conditions (Table 1). However, average soil moisture contents at 30 cm depth clearly reflected the dry spring in 2011.

3.2 ^{13}C enrichment in shoots and roots

The excess atom fraction (i.e. the ^{13}C enrichment compared to natural background levels) of the shoots peaked within the first hours after the labeling experiment in both years, in 2010 (ctrl: 0.25 ± 0.04 %, 6 h after pulse labeling; tmt: 0.10 ± 0.03 %, 0 h after pulse labeling; mean $\pm$ SE)

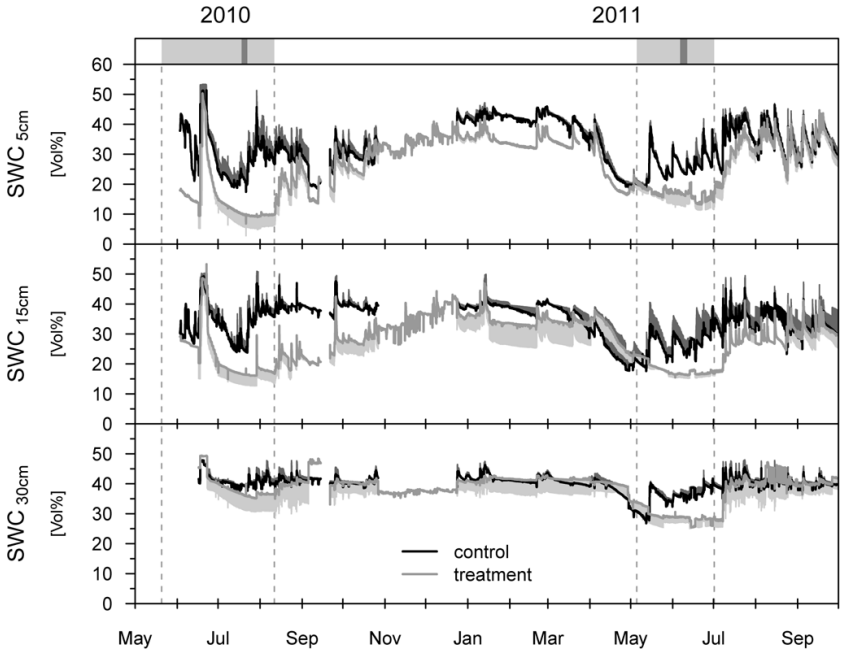

Fig. 2. Soil water content from May 2010 to October 2011 in 5 cm (top), 15 cm (middle) and 30 cm (bottom) soil depth for control (black) and treatment (grey) conditions. Lines represent mean, shading shows SE ($n = 3$) in one direction only to improve clearness. Lines without shading represent mean values from just one replicate ($n = 1$, due to sensor failure). The light grey rectangles and the inserted dark lines in the uppermost panel mark the shelter period (continued by vertical dashed lines into the other plots) and the days of the pulse labeling experiments, respectively.

and 2011 (ctrl: 0.12 ± 0.03 %, 0 h after pulse labeling; tmt: 0.13 ± 0.04 %, 0 h after pulse labeling; mean $\pm$ SE) (Fig. 3). However, the magnitude of the ^{13}C enrichment in shoots differed between the two years, as the control plots showed a much higher enrichment in 2010 compared to 2011. The drought stressed plots, on the other hand, showed comparable ^{13}C incorporation in shoots in both years. During the first four days after labeling, significant differences in the ^{13}C enrichment of shoots between drought and control plots were observed in 2010, but not in 2011 (see Fig. 3 for significance levels). During the full measurement campaign (i.e. 30 days after pulse labeling), the ^{13}C enrichment in shoots decreased steadily both under treatment and under control conditions in both years. In 2010, we even found ^{13}C label in above-ground biomass after the first cut, indicating remobilization of stored carbohydrates for regrowth while in 2011 no differences in ^{13}C enrichment were found during our campaign or after later cuts (data not shown).

Peak tracer appearance in roots (Fig. 3) was observed 1 to 2 days after pulse labeling under control conditions in both years, with the observed maximum being higher in 2010 compared to 2011 (2010: 0.015 ± 0.001 %, 22 h after pulse labeling; 2011: 0.009 ± 0.002 %, 34 h after pulse labeling; mean $\pm$ SE). Under the drought treatment, a first increase in ^{13}C enrichment of roots in both years occurred already two hours after pulse labeling, followed by a second increase 1 day after labeling (2010: 0.005 ± 0.003 %, 22 h after pulse labeling; 2011: 0.003 ± 0.001 %, 24 h after pulse labeling; mean $\pm$ SE). In general, roots in drought plots tended to show lower enrichments compared to those grown under control conditions. This difference was highly significant for roots sampled within the first day after pulse labeling in 2010, but not in 2011, when this difference was only significant for the peak enrichment on control plots 34 h after pulse labeling. During the full measurement campaign (i.e. up to 30 days), the enrichment in roots did not show the steady decrease observed for shoots (only under control conditions in 2011). Instead, it strongly fluctuated in 2010 for both treatment and control or stayed relatively constant in 2011 under drought conditions. ^{13}C enrichment in bulk soil samples was minor to undetectable, thus the results were excluded from further analyses.

3.3 ^{13}C excess in above- and below-ground biomass

In order to calculate the ^{13}C excess at the community level, we took standing above- and below-ground biomass at the time of the pulse labeling experiments into account (Table 2). Above-ground biomass 3 to 6 weeks after shelter set-up did not show any treatment effect in 2010 (1 July) nor in 2011 (26 May). However, above-ground biomass was much lower three weeks after shelter set-up in 2011 than in 2010, most likely due to the pronounced spring drought in 2011. Standing above-ground biomass 5 to 8 weeks after shelter

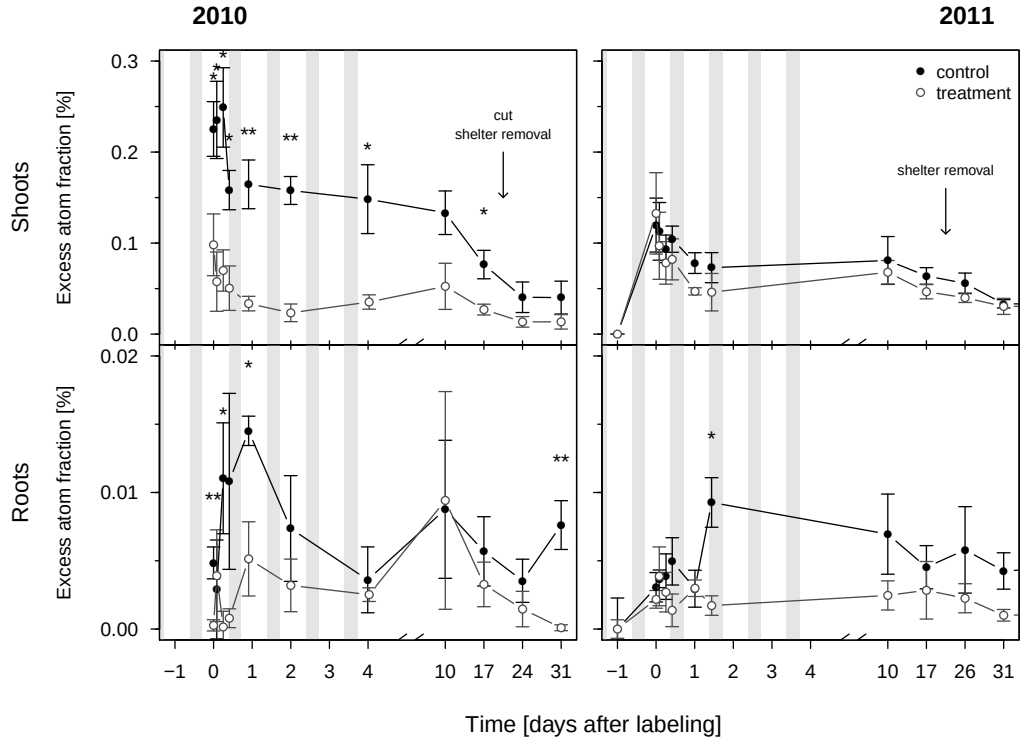

Fig. 3. ^{13}C enrichment expressed as excess atom fraction in percent in shoot (top) and root (bottom) biomass for 2010 (left) and 2011 (right) until 30 days after pulse labeling under control (filled symbols) and treatment (open symbols) conditions (mean ± SE; $n = 3$). Samples of > 4 days after labeling have all been taken at the same day, thus axis labels show the shortest time difference between sampling and pulse labeling (e.g. 10 days after labeling actually represent 10–12 days after labeling in 2010 and 10–13 days after labeling in 2011). Grey areas mark night-time. Stars show significant differences between control and treatment: * $p \leq 0.05$, ** $p \leq 0.01$.

set-up (during the pulse labeling experiments, approximated by linear interpolation) was comparable in 2010 and 2011 for the control plots (about 80 g m^{-2}), but was reduced in both years for the drought plots, with a stronger reduction in 2011 (about 76 %) compared to 2010 (43 %). Above-ground biomass grown within two weeks after shelter removal (until 25 August 2010 and 15 July 2011) was significantly reduced under drought conditions compared to control conditions in both years.

Standing below-ground biomass in the drought plots in 2010 was significantly higher (about a factor of four) than in the control plots 5 to 8 weeks after shelter set-up, but not in 2011. Nevertheless, standing below-ground biomass on control plots in 2011 was very similar to that on the drought plots and was considerably higher compared to 2010.

In both years 2010 and 2011, the effect of drought on above-ground ^{13}C incorporation became clearer after considering ^{13}C excess (and hence the respective biomass pools) (Fig. 4). Significantly higher ^{13}C excess was found for control compared to drought plots for almost all sampling points during the first four days after pulse labeling for both years (Fig. 4). In addition, the ^{13}C excess of control plots in above-ground biomass was almost twice as high in 2010 than in 2011, despite the estimated standing above-ground biomass being almost identical (Table 2). ^{13}C excess peaked at 82.9 ± 15.9 mg ^{13}C m^{-2} in 2010 and at 39.1 ± 9.3 mg ^{13}C m^{-2} (mean ± SE) in 2011 (control). Under drought conditions, the ^{13}C excess in above-ground biomass was only slightly higher in 2010 compared to 2011 and peaked at 19.3 ± 6.9 mg ^{13}C m^{-2} in 2010 and at 10.5 ± 3.4 mg ^{13}C m^{-2} in 2011 (mean ± SE). The Tukey HSD test showed no significant change over time for the control plots over the first four days after pulse labeling, while the first significant difference from the initial value was observed one day after pulse labeling for the drought plots in both years.

The effect of drought on ^{13}C excess in below-ground biomass was not significant in 2010, and only once in 2011, about 1.5 days after pulse labeling (Fig. 4). On the control plots, ^{13}C excess in below-ground biomass peaked at 6.1 ± 0.6 mg ^{13}C m^{-2} in 2010 and at 12.7 ± 2.8 mg ^{13}C m^{-2} in 2011 (mean ± SE). On the drought plots, two peaks were observed, with the second peak (1 day after pulse labeling) reaching maximum values of 6.9 ± 4.4 mg ^{13}C m^{-2} in 2010 and 3.8 ± 0.8 mg ^{13}C m^{-2} in 2011. No significant change was observed over time in both years.

Table 2. Mean standing above-ground biomass (at the time of cutting) and below-ground biomass (sampled) for 2010 and 2011 before and after the pulse labeling experiments as well as the linearly interpolated values that were used for calculating ^{13}C excess. SE is given in brackets ($n = 3$).

	Above-ground biomass			Below-ground biomass		
2010	Cut	Interpol.	Cut	Sampled	Interpol.	Sampled
Date	1 July	22 July	25 August	21 July	22 July	30 July
Ctrl [g m^{-2}]	116 (44)	83	218 (21)	114 (25)	113	101 (42)
Tmt [g m^{-2}]	114 (24)	47	123 (24)[a]	496 (113)[b]	484	390 (92)[b]
Tmt/Ctrl [%]	98	57	56	435	428	386
2011	Cut	Interpol.	Cut	Sampled	Interpol.	Sampled
Date	26 May	10 June	15 July	6 June	10 June	11 June
Ctrl [g m^{-2}]	44 (11)	79	261 (45)	226 (65)	336	364 (29)
Tmt [g m^{-2}]	41 (8)	19	62 (18)[a]	326 (106)	315	313 (92)
Tmt/Ctrl [%]	89	24	24	144	94	86

Letters denote significant differences between control and treatment ([a] $p \leq 0.01$, [b] $p \leq 0.05$).

The tracer recovery rate in roots, indicating allocation below ground relative to total tracer uptake, revealed higher allocation to roots on drought plots compared to control plots (control: 8.2 % in 2010, 35.2 % in 2011; drought (at the time of the second peak): 31.8 % in 2010, 41.5 % in 2011). After four days, between 2.2 % (2010) and 18.8 % (2011) of the tracer were still found in roots on control plots, compared to 43.2 % (2010) and 33.9 % (2011) on drought plots.

3.4 ^{13}C excess in soil CO_2 efflux

Average soil CO_2 efflux was around 5.5 µmol m^{-2} s^{-1} under control conditions (2010: 5.6 ± 2.3 µmol m^{-2} s^{-1}, 2011: 5.6 ± 3.0 µmol m^{-2} s^{-1}; mean $\pm$ SD) and around 2 µmol m^{-2} s^{-1} under drought conditions (2010: 2.6 ± 2.1 µmol m^{-2} s^{-1}, 2011: 2.1 ± 2.5 µmol m^{-2} s^{-1}; mean $\pm$ SD) over the whole measurement period (Fig. 5). Recovery of soil CO_2 efflux after shelter removal in 2010 (11 August 2010) was very fast, within a few days respiration rates were back to control conditions (no data are available after shelter removal in 2011).

The ^{13}C tracer appeared in soil CO_2 efflux immediately after pulse labeling on control plots as well as on drought plots, while ^{13}C excess in soil CO_2 efflux peaked during the first night after pulse labeling (Fig. 6). ^{13}C excess in soil CO_2 efflux was highest under control conditions in 2010, however, associated with a high variability due to the fact that two of the three control replicates were heavily impacted by mice (Orniplan, 2011). Therefore, they were excluded from further analysis. In both years 2010 and 2011, ^{13}C excess in soil CO_2 efflux was considerably reduced under drought conditions, with lowest ^{13}C excess values on drought plots in 2011. Relative tracer recovery rates in soil CO_2 efflux on control plots four days after pulse labeling were 48 % (2010) and 43 % (2011), and 36 % (2010) and 27 % (2011) on drought plots.

Calculating the cumulative ^{13}C excess for the entire measurement period showed an initial steep increase under control conditions, followed by a slow steady rise. Nineteen days after labeling, the cumulative ^{13}C excess in soil CO_2 efflux on control plots was 61.9 mg m^{-2} in 2010 (no SE available as only one replicate could be used) and 28.5 ± 7.9 mg m^{-2} in 2011 (mean $\pm$ SE), with mean recovery rates of 80 % (2010) and 73 % (2011). In contrast, 19 days after pulse labeling, cumulative ^{13}C excess in soil CO_2 efflux on drought plots reached only 11.0 ± 2.8 mg m^{-2} in 2010 and 6.3 ± 3.3 mg m^{-2} in 2011 (mean $\pm$ SE), with mean recovery rates of 57 % in 2010 and 60 % (2011).

4 Discussion

4.1 Below-ground carbon allocation under control conditions

^{13}C enrichment as well as ^{13}C excess in shoots and roots on control plots showed a fast below-ground allocation of newly fixed photoassimilates, as ^{13}C signals in roots were observed within 1–2 days after pulse labeling. Tracer also appeared in soil CO_2 efflux within the first hours after labeling, while maximum ^{13}C excess was observed already in the first night after pulse labeling. These results suggest a fast coupling between above- and below-ground systems (reviewed by Kuzyakov and Gavrichkova, 2010) and support results from other field experiments on grassland (Bahn et al., 2009; De Deyn et al., 2011; Ostle et al., 2000; Leake et al., 2006). More recent assimilates were used for soil CO_2 efflux than incorporated or stored in roots within the first four days after labeling. A rather slow decrease of ^{13}C excess in shoots suggested that quite a large fraction of fresh assimilates was kept in above-ground plant parts. Short-term storage under control conditions might have been responsible for this observation,

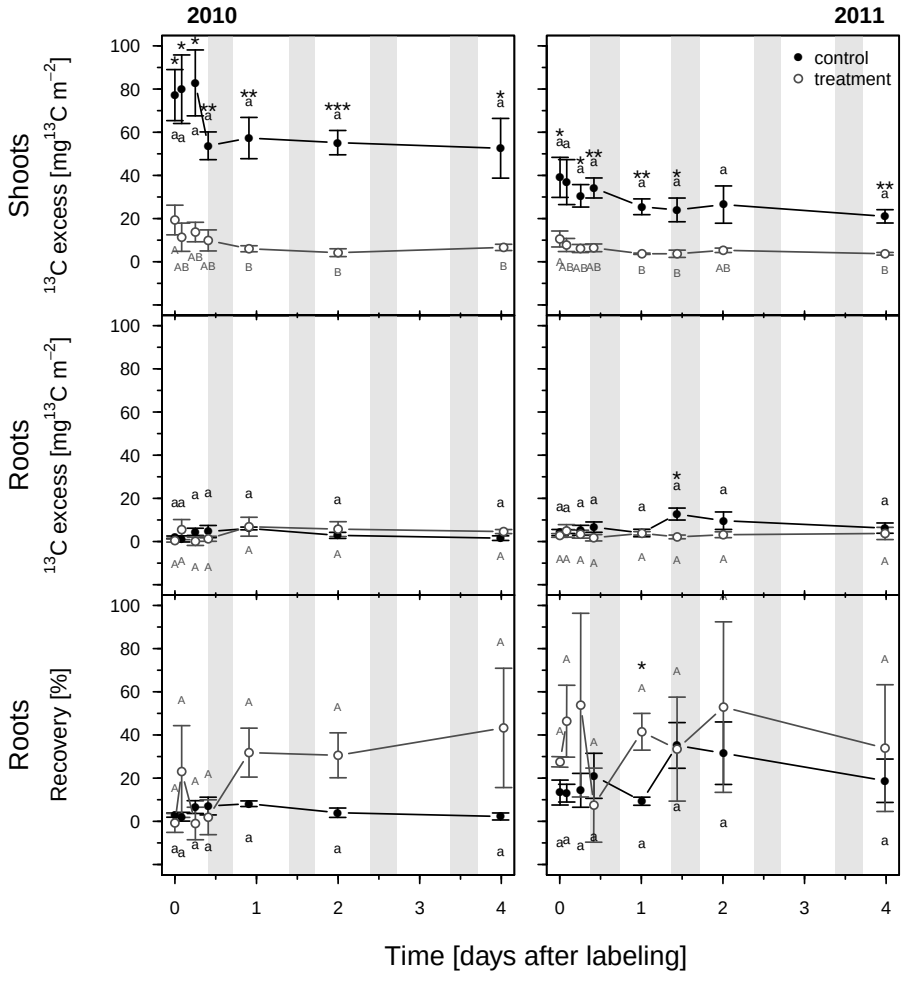

Fig. 4. ^{13}C excess [mg ^{13}C m^{-2}] in shoot (top) and root (middle) biomass at the community level as well as recovery rate in root biomass (bottom) for 2010 (left) and 2011 (right). Filled symbols: control plots; open symbols: treatment plots (mean ± SE, $n = 3$). Grey areas mark night-time. Stars show significant differences between control and treatment conditions: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. Letters denote results from Tukey HSD test (lowercase: control, capital: treatment): samples with the same letter show no significant difference within the treatment group.

supported by Bahn et al. (2013) who found a large and fast ^{13}C incorporation into starch which was subsequently used in the following night. Such transitory starch plays a large role as substrate for nocturnal respiration, as shown for example by Barthel et al. (2011a) for beech saplings (*Fagus sylvatica*) and for thale cress (*Arabidopsis thaliana)* in laboratory experiments (Zeeman et al., 2007). However, in our study, ^{13}C excess in shoots decreased rather slowly during the first four days after labeling. This suggested that either a large part of recent assimilates were directly used for above-ground growth or that assimilates were incorporated into short-term storage pools exceeding the respiratory demand in the first night after pulse labeling. The second hypothesis is supported by results from a laboratory experiment with perennial ryegrass (*Lolium perenne)* where short-term storage in leaves was much larger than that required to supply dark respiration during the night (Lehmeier et al., 2010). In addition, during the entire measurement campaign of 19 days, more than 73–80 % of ^{13}C taken up was lost to soil CO_2 efflux in 2010 and 2011, also supporting the storage pool hypothesis. No tracer was found in shoots after the 2nd cut in 2011 (125 days after pulse labeling).

4.2 Drought effects on below-ground carbon allocation

Drought stress resulted in a lower ^{13}C excess of shoots in both years, while below-ground allocation was not negatively affected. Much in contrast, the decrease of ^{13}C in shoots during the first four days after pulse labeling and the subsequent increase in below-ground ^{13}C enrichment showed a proportionally higher allocation of recent assimilates to roots under drought compared to control conditions. Our observation of lower ^{13}C excess under drought is in line with lower

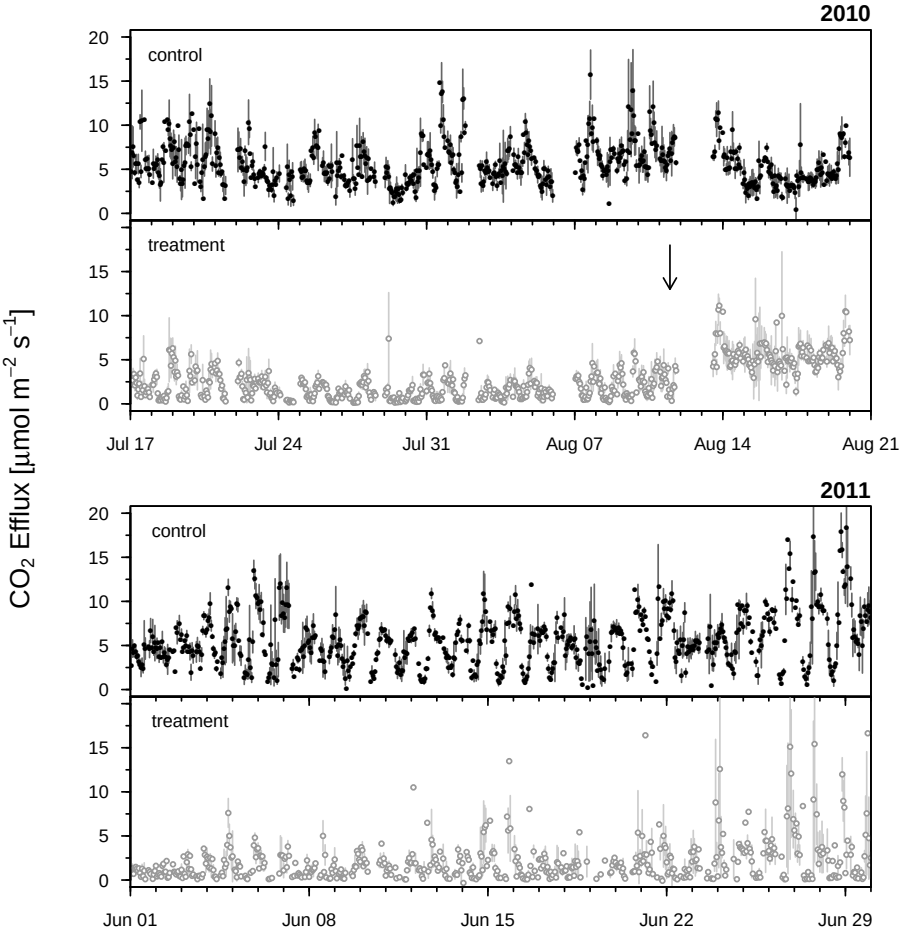

Fig. 5. Time series of soil CO_2 efflux for the measurement periods in 2010 (top) and 2011 (bottom). Arrow marks shelter removal in 2010. Filled symbols: control; open symbols: treatment (mean ± SE), averaged from three replicates. For values with no SE, only n=1 was available.

assimilation rates measured at this site (C. Bollig, University of Berne, personal communication, 2012; Signarbieux and Feller, 2011). However, while these findings contradict results from beech saplings labeled in the greenhouse where drought stress doubled the residence time of fresh assimilates in foliar biomass (Ruehr et al., 2009), higher allocation of recent assimilates to roots under drought conditions have been reported for grassland communities grown under laboratory conditions (Huang and Fu, 2000; Sanaullah et al., 2012), wheat grown in a greenhouse (Palta and Gregory, 1997) as well as beech saplings grown in climate chambers (Barthel et al., 2011a). Thus, differences in plant functional type or severity of drought stress might contribute to these differences. In addition, our results are supported by findings of increased standing root biomass under drought conditions at our grassland site (U. Prechsl, ETH Zurich, personal communication, 2013), also indicating that fresh assimilates transported below ground were preferentially used for root growth in response to drought stress, most probably to increase the possibility of plants foraging for water. Our findings are also in accordance with results from extensively managed grasslands where below-ground productivity was enhanced under summer drought (Kahmen et al., 2005).

The use of fresh assimilates for soil CO_2 efflux was not delayed under drought stress but reduced in absolute (excess$^{13}C_F$) terms in both years 2010 and 2011. The increase in cumulative ^{13}C excess was slower and we observed a trend towards lower recovery (Recovery$_F$) under drought compared to control conditions four days after labeling. This trend became slightly clearer 19 days after pulse labeling, when the contribution of freshly assimilated carbon to soil CO_2 efflux was around 60 % in both years, compared to about 75 % under control conditions. Thus, despite higher allocation below ground under drought, recent assimilates were not used equally fast for respiration as on control plots. These results support our findings that proportionally more fresh assimilates were invested into root growth under drought, in line with common knowledge that root growth is

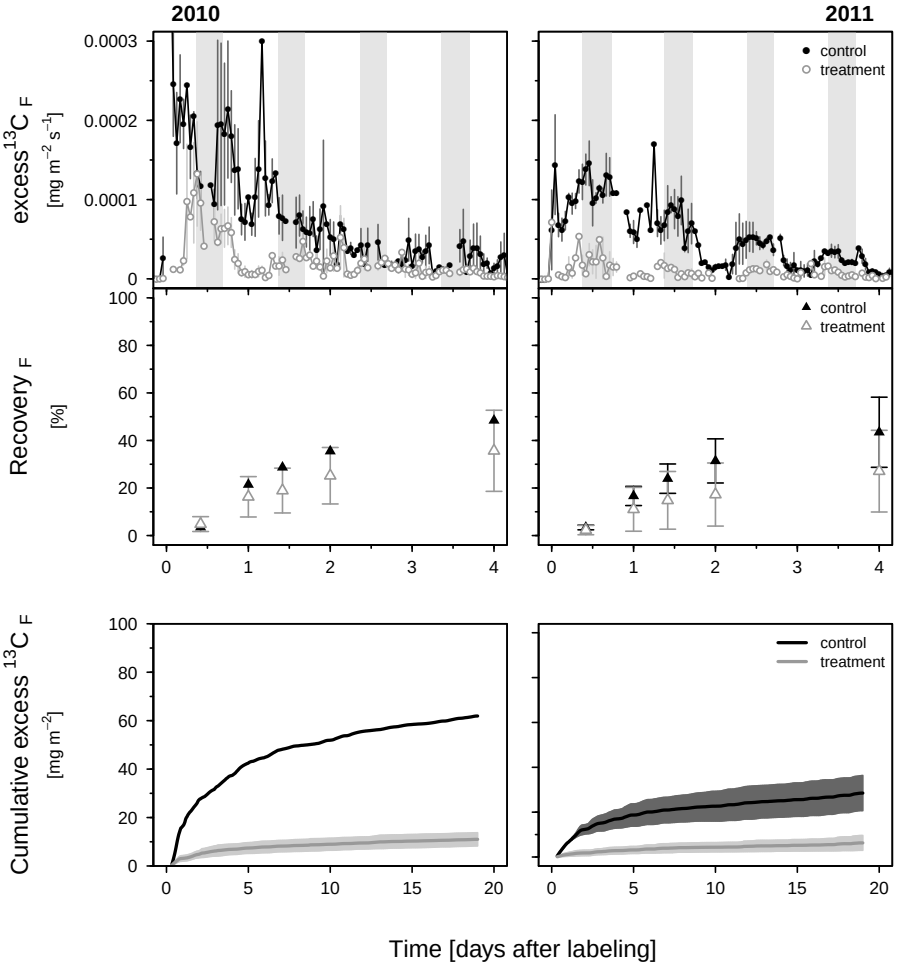

Fig. 6. Top panel: ^{13}C excess [mg ^{13}C m^{-2}] in soil CO_2 efflux (mean ± SE, $n = 3$) during the first 4 days after pulse labeling. Grey areas mark night-time. Middle panel: recovery rate in soil CO_2 efflux at the sampling times of shoot and root biomass (Fig. 4) during the first 4 days after pulse labeling (error bars show the propagated standard error). Lower panel: cumulative excess in soil CO_2 efflux (mean ± SE; control 2010: $n = 1$, treatment 2010: $n = 3$; control and treatment 2011: $n = 2$) until 19 days after pulse labeling. Left: 2010, right: 2011. Filled symbols: control, open symbols: treatment.

less affected by drought stress compared to leaf growth and that root growth might even increase when soil moisture is limiting (Lambers et al., 2006).

However, with increased root growth under drought conditions, one could also hypothesize that root respiration should increase due to higher growth respiration. But our results do not allow to clearly test this hypothesis, because fresh assimilates cannot only be used for root growth or root respiration, but can also be stored in root or allocated to (and immobilized by) microorganisms via exudates (Brüggemann et al., 2011). In addition, different carbon pools can be used for these competing sink processes (Lehmeier et al., 2010; Bahn et al., 2013). Thus, different below-ground processes contributing to total soil CO_2 efflux (measured in this study) would need to be partitioned in terms of the use of fresh assimilates. Such a flux partitioning is complex and would require a very different experimental set-up, well beyond the scope of this study.

Nevertheless, our results agree well with previous studies where rapid changes in allocation strategy were observed in response to drought (Sanaullah et al., 2012; Huang and Fu, 2000; Barthel et al., 2011a; Ruehr et al., 2009; Palta and Gregory, 1997) as well as with shading or clipping experiments (Craine et al., 1998; Wan and Luo, 2003; Bahn et al., 2009; Bahn et al., 2013). For example, CO_2 efflux was often clearly reduced in response to the respective treatment in these grassland clipping and shading experiments (Craine et al., 1998; Wan and Luo, 2003; Bahn et al., 2009), while no change in allocation speed was observed in a mountain grassland in response to shading, presumably to maintain allocation below ground under shading at the expense of above-ground carbon pools (Bahn et al., 2013).

In summary, we found a reduced coupling of above- and below-ground systems in grassland under drought stress compared to control conditions. Our data of root growth, tracer recovery in roots and soil CO_2 efflux of drought-stress swards in the field supported the second explanation of our hypothesis, that is, higher relative below-ground allocation of recent assimilates in response to summer drought, while keeping C loss via root respiration low.

4.3 Comparison of the two years 2010 and 2011

During our 2 yr experiment, Switzerland was hit by a spring drought in 2011 (MeteoSwiss, 2012). One could argue that the consequences of this extreme event might have affected the C cycling in our grassland in 2011 compared to 2010, as the plots showed signs of drought stress before the pulse labeling experiments took place in early summer. Control plots showed less ^{13}C incorporation into shoots and a lower absolute ^{13}C excess in soil CO_2 efflux in 2011. In addition, we observed a tendency towards higher below-ground C allocation and increased standing below-ground biomass in 2011 compared to 2010. Consequently, the differences between control and drought conditions were less pronounced in 2011 than in 2010. It is well known that growth (and hence growth respiration) is the first physiological process to be negatively affected by drought, followed by a reduction in photosynthesis, and thereafter by a reduction in maintenance respiration, leading to an initial surplus of carbohydrates at the beginning of a drought (McDowell, 2011; Koerner, 2012; Lambers et al., 2006). This surplus of carbohydrates can induce higher C allocation below ground as indeed observed under drought conditions both in 2010 and 2011. Furthermore, Wolf et al. (2013) could show a reduction in gross primary productivity at the same site during the spring drought in 2011 compared to 2010 using eddy-covariance measurements. Taken altogether: although there was a response to a natural drought in spring 2011, it was much smaller than the response to the experimental droughts in 2010 and 2011. With responses to both drought conditions being highly comparable, this "natural experiment" actually increases the confidence in the generalizability of our findings.

Acknowledgements. Funding was received from the European Community's Seventh Framework Programme (FP7/2007-2013) under grant agreement no. 226701 (CARBO-Extreme). We would like to thank Annika Ackermann and Roland Werner for sample analysis in the Grassland Sciences Isolab at ETH Zurich and Peter Plüss, Thomas Baur and Patrick Flütsch for technical support in the field and at ETH Zurich. We thank Hans-Ruedi Wettstein and the employees at the ETH research station Chamau for their cooperation. Moreover, thanks to Rebecca Hiller, Jacqueline Stieger and Sabina Keller for provision of meteorological data, and to Michael Bahn and Michel Schmitt (University of Innsbruck, Austria) for sharing knowledge on pulse labeling experiments in the field. We also highly appreciate the comments from two anonymous reviewers, improving an earlier version of our manuscript.

Edited by: C. Williams

References

Bahn, M., Schmitt, M., Siegwolf, R., Richter, A., and Brüggemann, N.: Does photosynthesis affect grassland soil-respired CO_2 and its carbon isotope composition on a diurnal timescale?, New Phytol., 182, 451–460, doi:10.1111/j.1469-8137.2008.02755.x, 2009.

Bahn, M., Lattanzi, F. A., Hasibeder, R., Wild, B., Koranda, M., Danese, V., Brüggemann, N., Schmitt, M., Siegwolf, R., and Richter, A.: Responses of belowground carbon allocation dynamics to extended shading in mountain grassland, New Phytol., 198, 116–126, doi:10.1111/nph.12138, 2013.

Barthel, M., Hammerle, A., Sturm, P., Baur, T., Gentsch, L., and Knohl, A.: The diel imprint of leaf metabolism on the $\delta^{13}C$ signal of soil respiration under control and drought conditions, New Phytol., 192, 925–938, doi:10.1111/j.1469-8137.2011.03848.x, 2011a.

Barthel, M., Sturm, P., and Knohl, A.: Soil matrix tracer contamination and canopy recycling did not impair $^{13}CO_2$ plant–soil pulse labelling experiments, Isot. Environ. and Healt., 47, 359–371, doi:10.1080/10256016.2011.587610, 2011b.

Brüggemann, N., Gessler, A., Kayler, Z., Keel, S. G., Badeck, F., Barthel, M., Boeckx, P., Buchmann, N., Brugnoli, E., Esperschutz, J., Gavrichkova, O., Ghashghaie, J., Gomez-Casanovas, N., Keitel, C., Knohl, A., Kuptz, D., Palacio, S., Salmon, Y., Uchida, Y., and Bahn, M.: Carbon allocation and carbon isotope fluxes in the plant-soil-atmosphere continuum: a review, Biogeosciences, 8, 3457–3489, doi:10.5194/bg-8-3457-2011, 2011.

CH2011: Swiss Climate Change Scenarios CH2011, C2SM, MeteoSwiss, ETH, NCCR Climate, OcCC, Zurich, CH, 88 pp., 2011.

Christensen, J. H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I., Jones, R., Kolli, R. K., Kwon, W.-T., Laprise, R., Magaña Rueda, V., Mearns, L., Menéndez, C. G., Räisänen, J., Rinke, A., Sarr, A., and Whetton, P.: Regional 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 Millers, H. L., Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 847–940, 2007.

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, doi:10.1038/nature03972, 2005.

Coplen, T. B.: Guidelines and recommended terms for expression of stable-isotope-ratio and gas-ratio measurement results, Rapid Commun. Mass Sp., 25, 2538–2560, doi:10.1002/rcm.5129, 2011.

Craine, J. M., Wedin, D. A., and Chapin, F. S.: Predominance of ecophysiological controls on soil CO_2 flux in a Minnesota grassland, Plant Soil, 207, 77–86, doi:10.1023/A:1004417419288, 1998.

De Deyn, G. B., Quirk, H., Oakley, S., Ostle, N., and Bardgett, R. D.: Rapid transfer of photosynthetic carbon through the plant-soil system in differently managed grasslands, Biogeosciences Discuss., 8, 921–940, doi:10.5194/bgd-8-921-2011, 2011.

Epron, D., Bahn, M., Derrien, D., Lattanzi, F. A., Pumpanen, J., Gessler, A., Hogberg, P., Maillard, P., Dannoura, M., Gerant, D., and Buchmann, N.: Pulse-labelling trees to study carbon allocation dynamics: a review of methods, current knowledge and future prospects, Tree Physiol., 32, 776–798, doi:10.1093/treephys/tps057, 2012.

Finger, R., Gilgen, A. K., Prechsl, U. E., and Buchmann, N.: An economic assessment of drought effects on three grassland systems in Switzerland, Reg. Environ. Change, 13, 365–374, doi:10.1007/s10113-012-0346-x, 2013.

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, doi:10.5194/bg-6-2525-2009, 2009.

Gilgen, A. K., Signarbieux, C., Feller, U., and Buchmann, N.: Competitive advantage of *Rumex obtusifolius* L. might increase in intensively managed temperate grasslands under drier climate, Agr. Ecosyst. Environ., 135, 15–23, doi:10.1016/j.agee.2009.08.004, 2010.

Hopkins, A. and Del Prado, A.: Implications of climate change for grassland in Europe: impacts, adaptations and mitigation options: a review, Grass Forage Sci., 62, 118–126, doi:10.1111/j.1365-2494.2007.00575.x, 2007.

Huang, B. R. and Fu, J. M.: Photosynthesis, respiration, and carbon allocation of two cool-season perennial grasses in response to surface soil drying, Plant Soil, 227, 17–26, doi:10.1023/a:1026512212113, 2000.

IPCC: Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaption, in: A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change (IPCC), edited by: Field, C. B., Barros, V., Stocker, T. F., Qin, D., Dokken, D. J., Ebi, K. L., Mastrandrea, M. D., Mach, K. J., Plattner, G.-K., Allen, S. K., Tignor, M., and Midgley, P. M., Cambridge University Press, Cambridge, UK and New York, NY, USA, 582, 2012.

Joos, O., Hagedorn, F., Heim, A., Gilgen, A. K., Schmidt, M. W. I., Siegwolf, R. T. W., and Buchmann, N.: Summer drought reduces total and litter-derived soil CO_2 effluxes in temperate grassland – clues from a 13C litter addition experiment, Biogeosciences, 7, 1031–1041, doi:10.5194/bg-7-1031-2010, 2010.

Kahmen, A., Perner, J., and Buchmann, N.: Diversity-dependent productivity in semi-natural grasslands following climate perturbations, Funct. Ecol., 19, 594–601, doi:10.1111/j.1365-2435.2005.01001.x, 2005.

Koerner, C.: Was steuert das Pflanzenwachstum?, Biologie in unserer Zeit, 42, 238–243, 2012.

Kuzyakov, Y. and Gavrichkova, O.: Time lag between photosynthesis and carbon dioxide efflux from soil: a review of mechanisms and controls, Glob. Change Biol., 16, 3386–3406, doi:10.1111/j.1365-2486.2010.02179.x, 2010.

Lambers, H., Chapin, F. S., and Pons, T. L.: Plant Physiological Ecology, Springer Science + Business Media, New York, USA, 540 pp., 2006.

Leake, J. R., Ostle, N. J., Rangel-Castro, J. I., and Johnson, D.: Carbon fluxes from plants through soil organisms determined by field $^{13}CO_2$ pulse-labelling in an upland grassland, Appl. Soil Ecol., 33, 152–175, doi:10.1016/j.apsoil.2006.03.001, 2006.

Lehmeier, C. A., Lattanzi, F. A., Gamnitzer, U., Schäufele, R., and Schnyder, H.: Day-length effects on carbon stores for respiration of perennial ryegrass, New Phytol., 188, 719–725, doi:10.1111/j.1469-8137.2010.03457.x, 2010.

McDowell, N. G.: Mechanisms Linking Drought, Hydraulics, Carbon Metabolism, and Vegetation Mortality, Plant Physiol., 155, 1051–1059, doi:10.1104/pp.110.170704, 2011.

MeteoSwiss: Klimabulletin Jahr 2011, Zurich, CH, 12 pp., 2012.

Nelson, D. D., McManus, J. B., Herndon, S. C., Zahniser, M. S., Tuzson, B., and Emmenegger, L.: New method for isotopic ratio measurements of atmospheric carbon dioxide using a 4.3 μm pulsed quantum cascade laser, Appl. Phys. B-Lasers O., 90, 301–309, doi:10.1007/s00340-007-2894-1, 2008.

Orniplan: Ornithologisches Inventar der landwirtschaftlichen Nutzfläche Kanton Zug, Erhebung 2010/2011, Baudirektion des Kantons Zug (Amt für Raumplanung), Zug, 35 pp., 2011.

Ostle, N., Ineson, P., Benham, D., and Sleep, D.: Carbon assimilation and turnover in grassland vegetation using an in situ $^{13}CO_2$ pulse labelling system, Rapid Commun. Mass Sp., 14, 1345–1350, doi:10.1002/1097-0231(20000815)14:15<1345::AID-RCM22>3.0.CO;2-B, 2000.

Ostle, N. J., Smith, P., Fisher, R., Ian Woodward, F., Fisher, J. B., Smith, J. U., Galbraith, D., Levy, P., Meir, P., McNamara, N. P., and Bardgett, R. D.: Integrating plant–soil interactions into global carbon cycle models, J. Ecol., 97, 851–863, doi:10.1111/j.1365-2745.2009.01547.x, 2009.

Palta, J. A. and Gregory, P. J.: Drought affects the fluxes of carbon to roots and soil in ^{13}C pulse-labelled plants of wheat, Soil Biol. Biochem., 29, 1395–1403, doi:10.1016/s0038-0717(97)00050-3, 1997.

Rayment, M. B. and Jarvis, P. G.: An improved open chamber system for measuring soil CO_2 effluxes in the field, J. Geophys. Res.-Atmos., 102, 28779–28784, doi:10.1029/97JD01103, 1997.

Reyer, C. P. O., Leuzinger, S., Rammig, A., Wolf, A., Bartholomeus, R. P., Bonfante, A., de Lorenzi, F., Dury, M., Gloning, P., Abou Jaoude, R., Klein, T., Kuster, T. M., Martins, M., Niedrist, G., Riccardi, M., Wohlfahrt, G., de Angelis, P., de Dato, G., Francois, L., Menzel, A., and Pereira, M.: A plant's perspective of extremes: terrestrial plant responses to changing climatic variability, Global Change Biol., 19, 75–89, doi:10.1111/gcb.12023, 2013.

Roth, K.: Bodenkartierung und GIS-basierte Kohlenstoffinventur von Graslandböden: Untersuchungen an den ETH-Forschungsstationen Chamau und Früebüel (ZG, Schweiz), Diploma Thesis, University of Zurich, Switzerland, Zurich, 132 pp., 2006.

Ruehr, N. K., Offermann, C. A., Gessler, A., Winkler, J. B., Ferrio, J. P., Buchmann, N., and Barnard, R. L.: Drought effects on allocation of recent carbon: from beech leaves to soil CO_2 efflux, New Phytol., 184, 950–961, doi:10.1111/j.1469-8137.2009.03044.x, 2009.

Sanaullah, M., Chabbi, A., Rumpel, C., and Kuzyakov, Y.: 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, 2012.

Seneviratne, S. I., Nicholls, N., Easterling, D., Goodess, C. M., Kanae, S., Kossin, J., Luo, Y., Marengo, J., McInnes, K., Rahimi, M., Reichstein, M., Sorteberg, A., Vera, C., and Zhang, X.: Changes in climate extremes and their impacts on the natural physical environment in: Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaption. A Special Report of Working Groups I and II of the Interngovernmental Panel on Climate Change (IPCC), edited by: Field, C. B., Barros, V., Stocker, T. F., Qin, D., Dokken, D. J., Ebi, K. L., Mastrandrea, M. D., Mach, K. J., Plattner, G.-K., Allen, S. K., Tignor, M., and Midgley, P. M., Cambridge University Press, Cambridge, UK, and New York, USA, 109–230, 2012.

Signarbieux, C. and Feller, U.: Non-stomatal limitations of photosynthesis in grassland species under artificial drought in the field, Environ. Exp. Bot., 71, 192–197, doi:10.1016/j.envexpbot.2010.12.003, 2011.

Sturm, P., Eugster, W., and Knohl, A.: Eddy covariance measurements of CO_2 isotopologues with a quantum cascade laser absorption spectrometer, Agr. Forest Meteorol., 152, 73–82, doi:10.1016/j.agrformet.2011.09.007, 2012.

Teuling, A. J., Seneviratne, S. I., Stöckli, R., Reichstein, M., Moors, E., Ciais, P., Luyssaert, S., van den Hurk, B., Ammann, C., Bernhofer, C., Dellwik, E., Gianelle, D., Gielen, B., Grünwald, T., Klumpp, K., Montagnani, L., Moureaux, C., Sottocornola, M., and Wohlfahrt, G.: Contrasting response of European forest and grassland energy exchange to heatwaves, Nat. Geosci., 3, 722–727, doi:10.1038/ngeo950, 2010.

van der Molen, M. K., Dolman, A. J., Ciais, P., Eglin, T., Gobron, N., Law, B. E., Meir, P., Peters, W., Phillips, O. L., Reichstein, M., Chen, T., Dekker, S. C., Doubková, M., Friedl, M. A., Jung, M., van den Hurk, B. J. J. M., de Jeu, R. A. M., Kruijt, B., Ohta, T., Rebel, K. T., Plummer, S., Seneviratne, S. I., Sitch, S., Teuling, A. J., van der Werf, G. R., and Wang, G.: Drought and ecosystem carbon cycling, Agr. Forest Meteorol., 151, 765–773, doi:10.1016/j.agrformet.2011.01.018, 2011.

Wan, S. Q. and Luo, Y. Q.: Substrate regulation of soil respiration in a tallgrass prairie: Results of a clipping and shading experiment, Global Biogeochem. Cy., 17, 1054, doi:10.1029/2002gb001971, 2003.

Wolf, S., Eugster, W., Ammann, C., Haeni, M., Zielis, S., Hiller, R., Stieger, J., Imer, D., Merbold, L., and Buchmann, N.: Contrasting response of grassland versus forest carbon and water fluxes to spring drought in Switzerland, Environ. Res. Lett., 8, 035007, doi:10.1088/1748-9326/8/3/035007, 2013.

Zeeman, S. C., Smith, S. M., and Smith, A. M.: The diurnal metabolism of leaf starch, Biochem. J., 401, 13–28, doi:10.1042/bj20061393, 2007.