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Drought impact on short-term carbon cycling in grassland

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The impact of extreme summer drought on the short-term carbon coupling of photosynthesis to soil CO₂ efflux in a temperate grassland

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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 $^{13}\text{CO}_2$ 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% $^{13}\text{CO}_2$ 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 shoots and increased carbon allocation below-ground relative to total tracer uptake. Contrary to our hypothesis, we did not find a change in allocation speed in response to drought, although drought clearly reduced soil CO_2 efflux rates. 19 days after pulse labeling, only about 60 % of total tracer uptake was lost via soil CO_2 efflux under drought compared to about 75 % under control conditions. Predisposition of grassland by spring drought lead to different responses to summer drought in 2011 compared to 2010, suggesting increased sensitivity of grassland to consecutive drought events as predicted under future climate change.

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 (Senevi-

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ratne et al., 2012). Drought events have recently gained importance in the discussion on climatic change and on 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 respiration, 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 wide-spread 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 heat-waves than forests: in contrast to forests, grasslands increase evaporation under solar radiation and temperature, not altering their water use efficiency (WUE), which ultimately leads to soil moisture depletion (Teuling et al., 2010;

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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 CO₂ efflux (Craine et al., 1998; Wan and Luo, 2003; Bahn et al., 2009), none of them has investigated the impact of drought so far. Drought-effects on below-ground carbon allocation of grasses have only been studied under laboratory conditions (Sanullah 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 ¹³CO₂ 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 respiration in response to a simulated extreme summer drought. Continuous measurements by quantum cascade laser spectroscopy enabled high temporal resolution measurements of soil CO₂ 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 CO₂ efflux. We hypothesized a tight coupling between above- and below-ground systems under normal conditions and expected the coupling to be reduced under drought stress, as it had been observed for beech saplings under drought (Ruehr et al., 2009; Barthel et al., 2011a).

2 Methods

2.1 Experimental setup

Experiments took place at a grassland in the Swiss lowlands, at Chamau, Switzerland (393 m a.s.l., 47°12' 37" N, 8°24' 38" E). The grassland is intensively managed, with up to six cuts per year, and regularly fertilized. It thus represents the wide-spread agricultural use of Swiss lowlands grasslands which is optimized for high fodder production. The original seed mixture consisted of smooth meadow-grass (*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 experimental setup was organized in a block-design, with each block consisting of a control (ctrl) and a drought-treated plot (tmt) which was covered by shelters during the treatment period. Plots 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 (ECH₂O 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 replicates, 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 replicate (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.

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We simulated summer drought for 8–12 weeks during the summer months with rain-out shelters (Table 1), which had an area of 3×3.5 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, Westerborg, DE). Two sides of the shelters were open to ensure sufficient air circulation. Underneath the shelters, core plot areas of 1×2 m were set up 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 $^{13}\text{CO}_2$ 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, $1 \text{ m} \times 1 \text{ m} \times 0.7 \text{ m}$), 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% $^{13}\text{CO}_2$ (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 $^{13}\text{CO}_2$ 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 cham-

ber 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 CO₂ 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 at 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 cm × 7 cm), and kept cool on ice until microwave treatment (see below). Then, a soil sample was taken with a soil core auger (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 ground and subsequently analyzed by isotope ratio mass spectrometry for $\delta^{13}\text{C}$ and C content.

2.4 Measurements of soil CO₂ efflux by laser spectroscopy

In order to trace carbon in soil CO₂ efflux, soil CO₂ 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 took place. Shallow PVC collars (with an inner diameters 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 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: $0.472 \pm 0.005 \text{ L min}^{-1}$; 2011: $0.536 \pm 0.002 \text{ L min}^{-1}$; mean \pm SD) from the soil chambers to the laser spectrometer, which was installed in a dedicated air conditioned shed 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 (for details, see Burri et al., in preparation). With this setup, it was possible to calculate soil CO₂ 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 CO₂ efflux chambers (mol s^{-1}), C_{out} ($\mu\text{mol mol}^{-1}$) the CO₂ concentration inside the soil CO₂ efflux chambers, C_{in} ($\mu\text{mol mol}^{-1}$) the CO₂ concentration of outside air, and A the ground area of the soil CO₂ efflux chambers (m^2). The ¹³C concentration of soil CO₂ efflux was calculated based on an isotopic mass balance approach, resulting in the respective $\delta^{13}\text{C}$ values

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$(\delta^{13}\text{C}_F)$:

$$\delta^{13}\text{C}_F = \frac{\delta^{13}\text{C}_{\text{out}} \cdot C_{\text{out}} - \delta^{13}\text{C}_{\text{in}} \cdot C_{\text{in}}}{C_{\text{out}} - C_{\text{in}}} \quad (2)$$

where

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

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

On 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 in soil respiration. 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 $\delta^{13}\text{C}$ was c. 0.33 ‰ in 2010 and c. 0.21 ‰ in 2011. For more detailed information on the chamber setup refer to Burri et al. (2013) and on calibration issues 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 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 $> 0.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ (according to the 95th percentile of the propagated error for control chambers in 2011) and values with propagated errors for the $\delta^{13}\text{C}$ of soil CO_2 efflux $> 35 \text{ ‰}$ (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

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

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

10 Where $x(^{13}\text{C})_{\text{plant}}$ refers to the atom fraction of the respective labeled plant sample and $x(^{13}\text{C})_{\text{plant(pre-lab)}}$ 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:

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

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

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

Where the $R(^{13}\text{C}/^{12}\text{C})_{\text{reference}}$ is the $^{13}\text{C} : ^{12}\text{C}$ isotope ratio of the international V-PDB standard. $\delta^{13}\text{C}_{\text{plant}}$ 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):

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

excess $^{13}\text{C}_{\text{plant}}$ [$\text{mg } ^{13}\text{C m}^{-2}$] is the amount of ^{13}C found in the respective pool of above- or belowground standing biomass. DW_{plant} refers to the standing biomass per square meter [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 $20 \text{ cm} \times 50 \text{ cm}$ 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 01 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 [$\text{mg } ^{13}\text{C m}^{-2} \text{ s}^{-1}$] beyond natural abundance values was determined as follows:

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

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

In order to obtain the cumulative excess $^{13}\text{C}_F$ until the end of the 1 month measurement period, gaps in excess $^{13}\text{C}_F$ were linearly interpolated, excess $^{13}\text{C}_F$ aggregated to hourly values and finally summed up. The first 8 h after label stop were excluded from the cumulative consideration as they had been shown to be strongly influenced by physical back-diffusion of the tracer signal (Burri et al., 2013). 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 average initial ^{13}C excess (0 h after label stop) found in shoots. The recovery in roots and soil CO_2 efflux was calculated as follows:

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

$$\text{Recovery}_F = \frac{\text{excess}^{13}\text{C}_F}{\text{excess}^{13}\text{C}_{\text{shoots},t0}} \quad (10)$$

These recovery rates should be considered as an approximation only, since total recovery sometimes summed up to $> 100\%$, most likely related to the uncertainty of the mean values used for these calculations.

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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 almost $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$. 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, however, 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: $0.25 \pm 0.04 \%$, 6 h after pulse labeling; tmt: $0.10 \pm 0.03 \%$, 0 h after

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pulse labeling; mean \pm SE) 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 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, during which 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

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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 into the shelter period did not show any treatment effect in 2010 (1 July 2010) nor in 2011 (26 May 2011). However, above-ground biomass was much lower three weeks into the shelter period in 2011 than in 2010, most likely due to the pronounced spring drought in 2011. In contrast, above-ground biomass grown until the first cut, two weeks after shelter removal, was significantly reduced under drought conditions compared to control conditions both in 2010 (25 August 2010) and 2011 (15 July 2011). Standing above-ground biomass 5 to 8 weeks into the shelter period (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 %).

Below-ground biomass varied strongly on a weekly to bi-weekly basis (Prechsl, ETH Zurich, personal communication, 2013). Yet, the effect of the drought treatment on standing below-ground biomass was not as consistent as on above-ground biomass. While we observed a trend towards increased below-ground biomass in response to drought in 2010, no such effect was found in 2011, also reflected in the interpolated values of below-ground biomass (Table 2).

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). The differences between drought and control became significant 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

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biomass being almost identical (Table 2). ^{13}C excess peaked at $82.9 \pm 15.9 \text{ mg } ^{13}\text{C m}^{-2}$ in 2010 and at $39.1 \pm 9.3 \text{ mg } ^{13}\text{C m}^{-2}$ (mean \pm SE) in 2011. Under drought conditions, the ^{13}C excess in above-ground biomass was only slightly higher in 2010 compared to 2011 and peaked at $19.3 \pm 6.9 \text{ mg } ^{13}\text{C m}^{-2}$ in 2010 and at $10.5 \pm 3.4 \text{ mg } ^{13}\text{C m}^{-2}$ in 2011 (mean \pm 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). At the control plots, ^{13}C excess in below-ground biomass peaked at $32.8 \pm 3.4 \text{ mg } ^{13}\text{C m}^{-2}$ in 2010 and at $12.7 \pm 2.8 \text{ mg } ^{13}\text{C m}^{-2}$ in 2011 (mean \pm SE). At the drought plots, two peaks were observed, while the second peak (1 day after pulse labeling) reached maximum values of $18.0 \pm 11.5 \text{ mg } ^{13}\text{C m}^{-2}$ in 2010 and $3.8 \pm 0.8 \text{ mg } ^{13}\text{C m}^{-2}$ in 2011. In general, ^{13}C excess in below-ground biomass was higher in 2010 compared to 2011, and showed no significant change over time.

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, especially in 2010 (control: 42 % in 2010, 32 % in 2011; drought: around 80 % in 2010, about 40 % in 2011). In addition, recovery rates were highly variable during the first day after labeling on drought plots in both years, and decreased steadily with time in 2010, but stayed relatively constant in 2011. After four days, between 11 % (2010) and 16 % (2011) of the tracer were still found in roots on control plots, compared to 62 % (2010) and 36 % (2011) on drought plots.

3.4 ^{13}C excess in soil CO_2 efflux

Average soil CO_2 efflux was around $5.5 \mu\text{mol m}^{-2} \text{ s}^{-1}$ under control conditions (2010: $5.6 \pm 2.3 \mu\text{mol m}^{-2} \text{ s}^{-1}$, 2011: $5.6 \pm 3.0 \mu\text{mol m}^{-2} \text{ s}^{-1}$; mean \pm SD) and

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around $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ under drought conditions (2010: $2.6 \pm 2.1 \mu\text{mol m}^{-2} \text{s}^{-1}$, 2011: $2.1 \pm 2.5 \mu\text{mol m}^{-2} \text{s}^{-1}$; 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 in soil CO_2 efflux on control plots four days after pulse labeling was 48 % (2010) and 43 % (2011), and 36 % (2010) and 27 % (2011) on drought plots. Summed up with the relative recovery in roots (Sect. 3.3), around 60 % of tracer were recovered on control plots and 60–100 % on drought plots after four days in both years.

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. 19 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 $28.5 \pm 7.9 \text{ mg m}^{-2}$ in 2011 (mean \pm SE), accounting for 80 % (2010) and 73 % (2011) of total ^{13}C recovery. 19 days after pulse labeling, cumulative ^{13}C excess in soil CO_2 efflux on drought plots reached $11.0 \pm 2.8 \text{ mg m}^{-2}$ in 2010 and $6.3 \pm 3.3 \text{ mg m}^{-2}$ in 2011 (mean \pm SE), accounting for 57 % in 2010 and 60 % (2011) of total ^{13}C recovery.

4 Discussion

4.1 Below-ground carbon allocation under control conditions

¹³C enrichment as well as ¹³C excess in shoots and roots on control plots showed a fast below-ground allocation of newly fixed photoassimilates, as ¹³C signals in roots were observed within 1–2 days after pulse labeling. Tracer also appeared in soil CO₂ efflux within the first hours after labeling, while maximum ¹³C 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 CO₂ efflux than incorporated or stored in roots within the first four days after labeling. A rather slow decrease of ¹³C 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, supported by Bahn et al. (2013) who found a large and fast ¹³C 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, ¹³C 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 ¹³C taken up was lost to soil CO₂ efflux

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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

Although drought stress resulted in a lower ^{13}C excess of shoots in both years, in line with lower assimilation rates (Bollig, University of Berne, personal communication, 2012), allocation below-ground was not negatively affected. On the contrary, the decrease of ^{13}C in shoots during the first four days after pulse labeling and the subsequent increase in the below-ground ^{13}C signals showed a proportionally higher allocation of recent assimilates to roots under drought compared to control conditions. This effect was particularly pronounced in 2010 (see below). Although 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 already have been reported for other grassland communities (Sanaullah et al., 2012) and wheat (Palta and Gregory, 1997). Differences in plant functional type or severity of the drought stress might contribute to these discrepancies. In addition, our results are supported by findings of increased standing root biomass under drought conditions at our grassland site (Prechsl, ETH Zurich, personal communication, 2013) and findings from extensively managed grasslands where below-ground productivity was enhanced under summer drought (Kahmen et al., 2005).

4.3 Drought effects on the use of fresh assimilates in soil CO_2 efflux

The use of fresh assimilates for soil CO_2 efflux was not delayed under drought stress but only reduced in both years 2010 and 2011, both in absolute (excess $^{13}\text{C}_F$) and relative (Recovery $_F$) terms. The increase in cumulative ^{13}C excess was slower and the recovery four days after labeling lower under drought compared to control conditions. Even after 19 days, the contribution of freshly assimilated carbon to soil CO_2 efflux

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was only 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 less affected by drought stress compared to leaf growth or that root growth might even increase when soil moisture is limiting (Lambers et al., 2006). Moreover, our results agree well with results from a mountain grassland where no change in allocation speed occurred in response to shading, presumably to maintain allocation below-ground under shading at the expense of above-ground carbon pools (Bahn et al., 2013). Thus, in our study, drought-stressed plants seemed rather to invest into root growth and keep C loss via root respiration low, while control plants used recently fixed carbon rather for root respiration than for root growth.

4.4 Comparison of the two years 2010 and 2011

Comparing our observations of the two years 2010 and 2011, two main aspects were strikingly different: first, ^{13}C incorporation into shoots under control conditions differed strongly between the two years. Second, the drought-induced increase in C allocation below-ground was more pronounced for 2010 than for 2011.

As Switzerland was hit by a spring drought in 2011 (MeteoSwiss, 2012), the consequences of this extreme event might have affected the C cycling in our grassland in 2011. The control plots showed clear signs of drought stress in 2011, although on a less severe level than the drought-stressed plots in 2010 and 2011: control plots showed less ^{13}C incorporation into shoots and a lower absolute ^{13}C excess in soil CO_2 efflux in 2011, but no increased below-ground allocation and no increase in standing below-ground biomass. Although environmental conditions were not fully comparable between the two years, it is most likely that the plots had not fully recovered from the spring drought before the pulse labeling experiments took place in early summer. 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 by eddy covariance measurements.

Furthermore, the effects of simulated summer drought were stronger in 2011 than in 2010 (stronger reduction in above-ground biomass, less ^{13}C incorporation into shoots, and slightly less ^{13}C recovery in soil CO_2 efflux), which might be a consequence of setting up the shelters on plots with already low soil moisture levels due to the spring drought. 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 observed in 2010. However, in 2011, drought plots seemed to be more severely hit by our simulated summer drought as the increase in allocation below-ground was lower compared to 2010. Thus, comparing the drought responses in 2010 and 2011 suggests that a spring drought preceding a summer drought might amplify the impact of summer drought on above-ground productivity as well as carbon allocation below-ground, thereby increasing the sensitivity of grassland to consecutive or reoccurring drought events – as predicted under future climate conditions.

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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 \pm SD).

Year		2010	2011	
Shelter duration		20 May–11 Aug	05 May–01 Jul	
Number of days		83	57	
Excluded precipitation [mm]		440 (39 %)	231 (21 %)	
Annual precipitation [mm]		1139	1084	
SWC [Vol%]	5 cm	Control	29.8 \pm 7.9	26.0 \pm 4.2
		Treatment	15.1 \pm 8.5	17.0 \pm 1.7
	tmt/ctrl [%]	51	65	
15 cm	Control	33.5 \pm 5.9	26.3 \pm 4.	
	Treatment	22.5 \pm 7.9	18.1 \pm 2.	
	tmt/ctrl [%]	67	69	
30 cm	Control	41.1 \pm 2.2	35.5 \pm 3.3	
	Treatment	38.9 \pm 3.9	29.2 \pm 1.9	
	tmt/ctrl [%]	95	82	

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Table 2. Mean standing above-ground biomass (at cuts) and below-ground biomass (sampled) for 2010 and 2011 before and after the pulse labeling experiments as well as the linearly interpolated value that was used for calculating ^{13}C excess. SE is given in brackets ($n = 3$).^a $p \leq 0.01$ denotes significance level.

2010 Date	Above-ground biomass			Below-ground biomass		
	Cut 1 Jul	Interpol. 22 Jul	Cut 25 Aug	Sampled 21 Jul	Interpol. 22 Jul	Sampled 30 Jul
Ctrl [g m^{-2}]	116 (44)	83	218 (21) ^a	635 (382)	607	386 (57)
Tmt [g m^{-2}]	114 (24)	47	123 (24)	1357 (595)	1270	572 (64)
Tmt/Ctrl [%]	98	57	56	214	209	148
2011 Date	Cut 26 May	Interpol. 10 Jun	Cut 15 Jul	Sampled 06 Jun	Interpol. 10 Jun	Sampled 11 Jun
Ctrl [g m^{-2}]	44 (11)	79	261 (45) ^a	225 (67)	335	362 (29)
Tmt [g m^{-2}]	41 (8)	19	62 (18)	325 (104)	315	313 (92)
Tmt/Ctrl [%]	89	24	24	144	94	86

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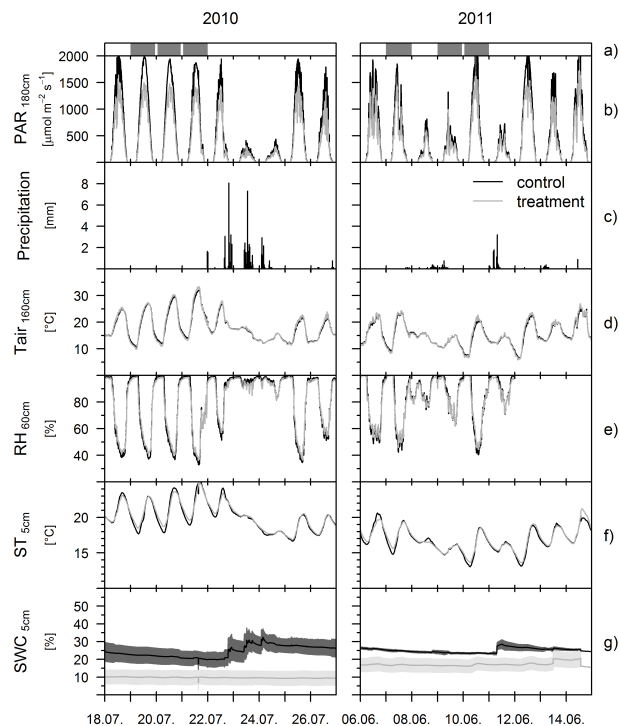


Fig. 1. Meteorological conditions during and shortly after pulse labeling experiments in 2010 (left) and 2011 (right) under control (black) and treatment (grey) conditions. **(a)** Grey shadings mark days of pulse labeling experiments, **(b)** Photosynthetically active radiation (PAR) at 180 cm height (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, $n = 3$).

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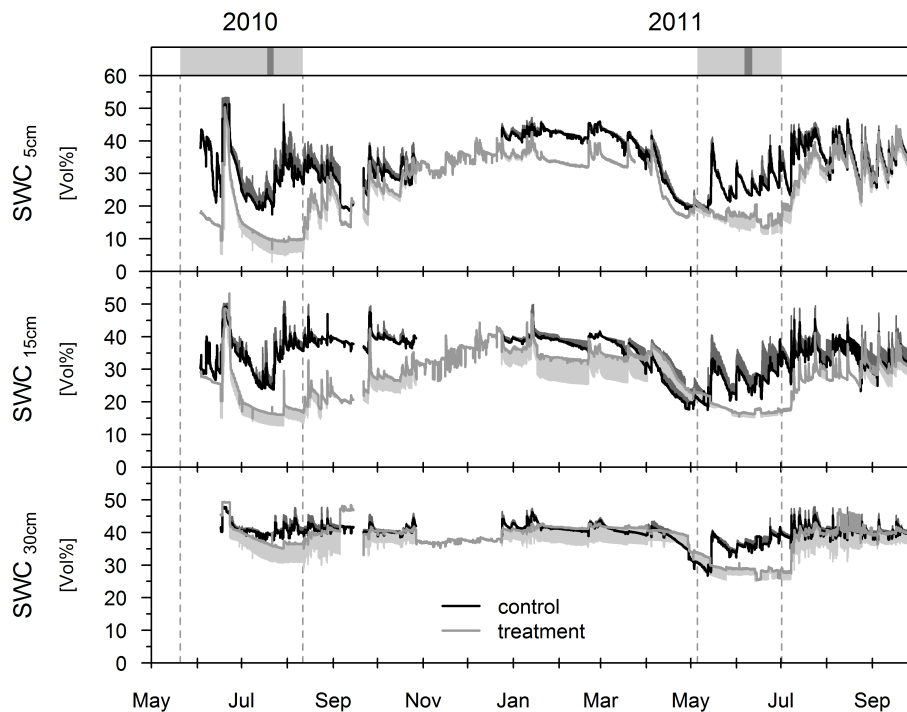


Fig. 2. Soil water content from May 2010 to October 2011 in 5 cm (top), 15 cm (middle) and 30 cm (bottom) soil depth for control (black) and treatment (grey) conditions. Lines represent mean, shading shows SE ($n = 3$) in one direction only to improve clearness. Lines without shading represent mean values 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.

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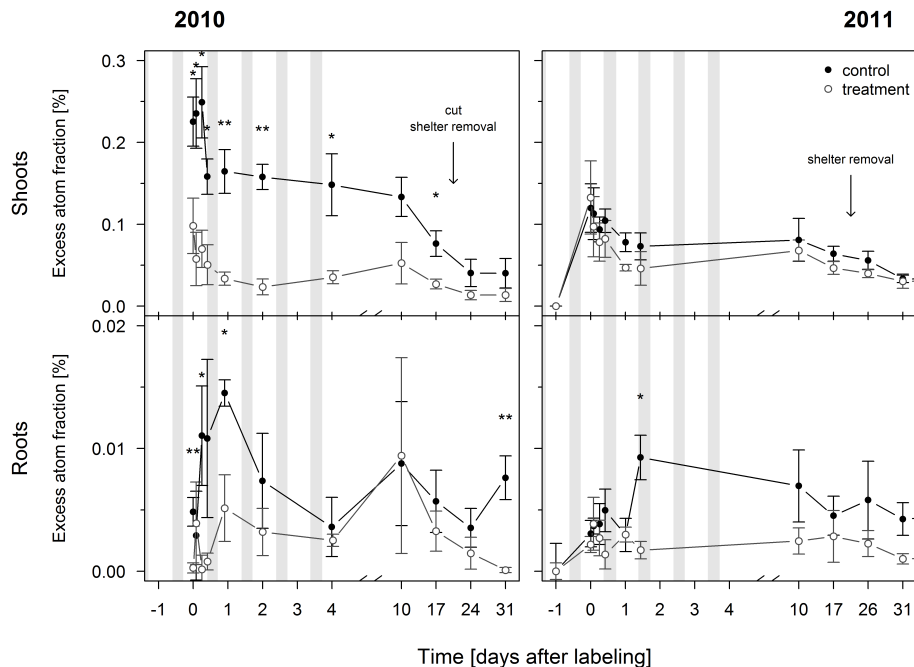


Fig. 3. ^{13}C enrichment expressed as excess atom fraction in percent in shoot (top) and root (bottom) biomass for 2010 (left) and 2011 (right) until 30 days after pulse labeling under control (black) and treatment (grey) conditions (mean \pm SE; $n = 3$). Samples of > 4 days after labeling have all 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: * $p \leq 0.05$, ** $p \leq 0.01$.

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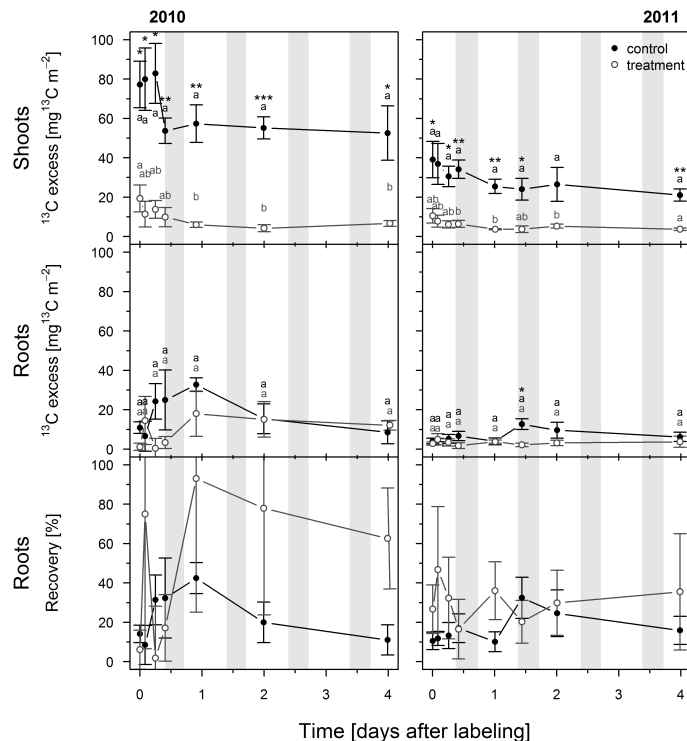


Fig. 4. ^{13}C excess [$\text{mg } ^{13}\text{C m}^{-2}$] in shoot (top) and root (middle) biomass at the community level as well as recovery rate in root biomass (bottom) for 2010 (left) and 2011 (right). Black: control plots; grey: treatment plots (mean \pm SE, $n = 3$); for Recovery_{roots} the propagated standard error is shown. Grey areas mark night-time. Stars show significance levels: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. Letters denote results from Tukey HSD Test: samples with the same letter are not significantly different from each other.

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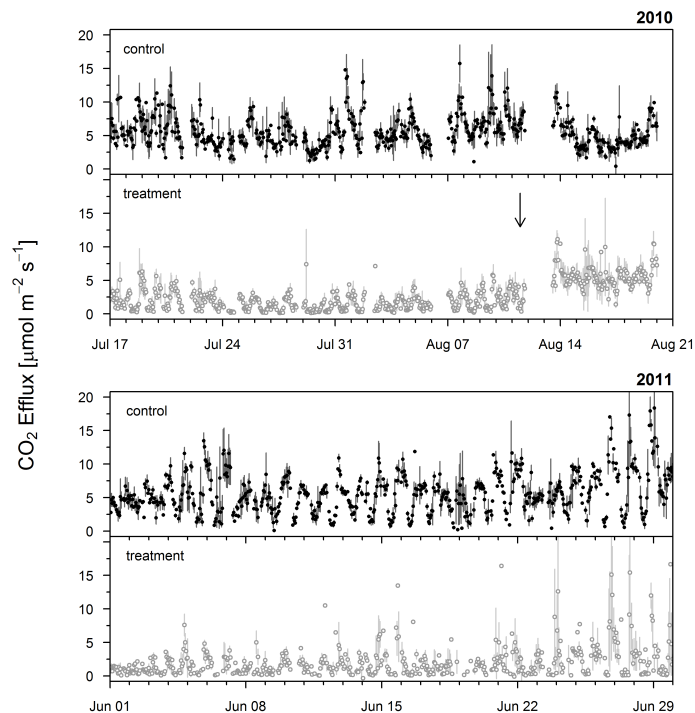


Fig. 5. Time series of soil CO₂ efflux for the measurement periods in 2010 (top) and 2011 (bottom). Arrow marks shelter removal in 2010. Black: control; grey: treatment (mean ± SE), averaged from three replicates. For values with no SE, only $n = 1$ was available.

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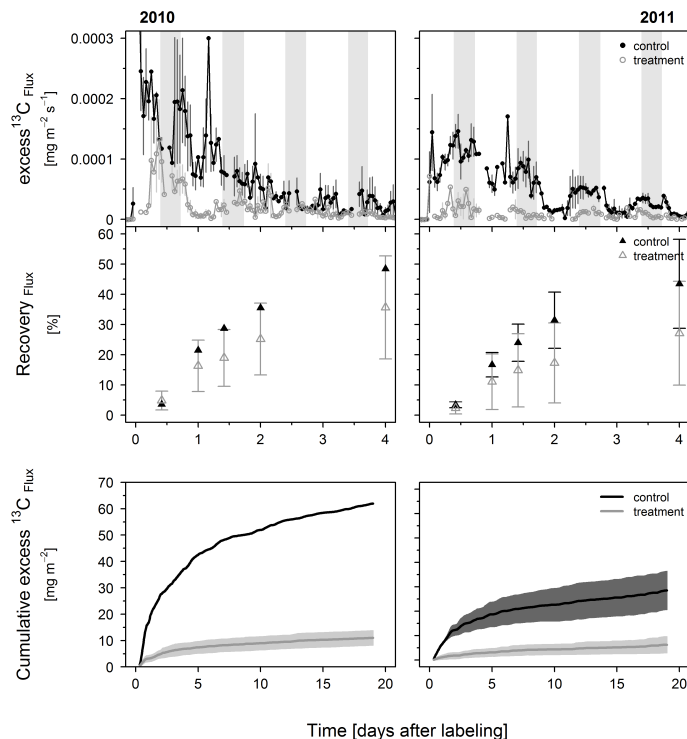


Fig. 6. Top panel: ^{13}C excess [$\text{mg } ^{13}\text{C m}^{-2}$] in soil CO_2 efflux (mean \pm SE, $n = 3$) during the first 4 days after pulse labeling. Grey areas mark night-time. Middle panel: Recovery rate in soil CO_2 efflux at the sampling times of shoot and root biomass (Fig. 4) during the first 4 days after pulse labeling (error bars show the propagated standard error). Lower panel: Cumulative excess in soil CO_2 efflux (mean \pm 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. Black: control, grey: treatment.