

Interactive comment on “The impact of extreme summer drought on the short-term carbon coupling of photosynthesis to soil CO₂ efflux in a temperate grassland” by S. Burri et al.

S. Burri et al.

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Response to Anonymous Referee #2

Referee: My overall assessment is that this study has been well performed and that the work is worthy of publication. The science was well implemented, the analyses and display are fitting and complete, and the writing is good. I have a few questions regarding interpretation outlined below but generally agree with what has been presented.

Response: We thank the referee for his/her highly positive judgment of our manuscript. His/her comments and questions lead us to critically evaluate our data, in particular the root biomass data again (see also comments to referee 1), which helped a lot in

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improving our manuscript.

Referee: Abstract: It would be appropriate to mention here the inferred shift in allocation of fresh assimilate to roots under drought conditions.

Response: Although this was already mentioned, we changed the text to make this point clearer as follows:

Former text: “Drought reduced the incorporation of recently fixed carbon into shoots and increased carbon allocation below-ground relative to total tracer uptake.”

Adapted text: “Drought reduced the incorporation of recently fixed carbon into shoots. However, the below-ground allocation of fresh assimilates relative to tracer uptake increased under the drought treatment.”

General Comments/Questions

Referee: The precipitation exclusion effectively removed summer precipitation and lowered soil water content in the upper 23 cm of soil. However, a significant fraction of roots active in water uptake could easily reside below this level in the soil where the soil moisture remained similar between control and treatment plots. Please discuss how this might influence your interpretation of the fumigation – tracer experiment.

Response: We fully understand the reviewer’s concern about this aspect. The difference in soil moisture at 30 cm depth between control and treatment was indeed on average not very high (Table 1). However, the course of soil moisture at 30 cm depth during the shelter period (Fig. 2) showed a distinct reduction in soil moisture at 30 cm at least in 2011. In addition, a companion study (Prechsl et al., mss in preparation) on the water uptake of grassland plants, conducted at the same site and on the same plots, showed that only about 5% (ctrl) and 3% (tmt) of total root biomass resided in 15-30 cm depth, while about 16% (ctrl) and about 8% (tmt) were in 5-15 cm depth and about 79% (ctrl) and 89% (tmt) resided in 0-5 cm depth (see cropped figure from this other manuscript in supplement "below-ground_biomass.pdf").

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Despite this low relative contribution of the deep soil layers, these roots might theoretically still play an important role in water uptake. But the same study (Prechsl et al.) could also show that, based on stable water isotope analysis of soil and xylem water of plants and much in contrast to our expectations, grassland plants strongly relied on the top 0-10 cm of the soil during the drought treatment (see cropped figure in supplement "below-ground_biomass.pdf").

In addition, if the drought-stressed plants would have used soil moisture from 30 cm depth, we would have expected a weaker or no drought response at all. However, we saw clear impacts of drought like reduced above-ground biomass, reduced carbon assimilation and also reduced above-ground ^{13}C excess, reduced soil respiration etc.

Referee: The major findings and key interpretations rely importantly on the estimate of community-level biomass above- and below-ground. Fig 3 shows clear differences between root excess atom fraction as percent, but these disappear when translated to the community-level because the treatment plots have twice as much root biomass (Table 2). Though the below-ground biomass is not significantly different at the stringent p-level of 0.01, the means are still very different and this is what was applied to estimate the key result of ^{13}C excess in shoot and root biomass at the community level (Fig 4). This raises the following questions, the answers to which could alter the paper's interpretations and conclusions: How would your interpretation of allocation patterns change if, given the lack of significant differences in belowground biomass between control and treatment plots, you pooled these data to provide a single mean belowground biomass across the two and used this mean to estimate ^{13}C excess at the community level? Would the apparent lack of ^{13}C excess at the community-level persist (as reported) or would the elevated root excess ^{13}C shown in Fig 3 lead to quite different conclusions? How was root biomass density sampled? Section 2.3 provides some mention but could be more complete. It appears that this key variable was not well sampled. Why was root biomass so much higher in the treatment compared to control plots?

Response: We thank the referee for his/her critical evaluation of this aspect. As mentioned above, his/her comments and questions lead us to critically re-evaluate our data, in particular the root biomass data again (see also comments to referee 1). Although the results for the below-ground biomass in 2010 now have changed compared to the previous version (while the results for below-ground biomass in 2011 have changed only marginally), the results for below-ground biomass under the drought treatment in 2010 and 2011 resemble each other much more and the treatment effect in 2010 has become significant (Table 2 and document “Changes_Table2.pdf”) and therefore, we think that pooling the samples for control and drought plots would not be meaningful now. In 2011, no significant effect between treatment and control conditions appeared. We believe that this is due to the control plants also showing some level of drought stress (as a results of spring drought in 2011, as already discussed in section 4.4). We believe the root biomass to be higher under treatment conditions as a direct response to the drought stress. This was observed before under summer drought (Kahmen et al., 2005) and is in line with common knowledge that roots growth might increase when soil moisture is limiting (see sections 4.3 and 4.4). Root mass was sampled as described in 2.3, we weighed all samples before they were ground. We slightly adjusted the text to make this clearer.

This re-analysis also now resulted in different ^{13}C excess values for the below-ground biomass in 2010, and a recalculation of the recovery rates in 2010 and 2011. Accordingly, section 3.3 and Fig. 4 have been changed (see adapted Fig.4 and the file “Changes_Fig4.pdf” as attachment). Using the re-calculated data, we could recalculate recovery in roots in a more sophisticated way on the replicate level (before, it was an assumption based on the mean values) and we did this for both years (therefore recovery rates also changed in 2011 in Fig.4).

Overall, we think that our data has become much more consistent and the overall message of our manuscript is now more straightforward, as we see consistent drought responses for both years, and some level of drought stress for control plants in 2011.

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We, once more, thank the referee for the critical evaluation which highly improved our manuscript.

Referee: The drought-induced decline in ^{13}C excess appears consistent with what would be expected from soil water stress and would be nicely corroborated by data showing the alleged decrease in assimilation rates but these data have not been shown in this paper. Can that be included?

Response: The drought-induced decline in ^{13}C excess was indeed significant for above-ground biomass in both years. The data on assimilation cannot be shown in this manuscript as it was collected in the framework of a companion project (University of Berne), focusing on specific physiological responses to drought stress at the same site and on the same plots. There is a manuscript in preparations to cover these topics (Bollig et al. in prep). A previous study conducted at the same site had already shown reduced assimilation rates in response to drought (Signarbieux and Feller, 2011). We added this ref. to our text (section 4.2)

Referee: Section 4.2. The finding that belowground delivery of fresh assimilate was similar in control and drought treatment plots, if not higher in the droughted plots, despite lower assimilation rates inferred for the droughted plots appears to suggest a rapid change in allocation strategy that increased root production to forage for water. It would be nice to see a slightly expanded discussion of this interpretation here, drawing on other literature and also slightly further exploring the contradiction with what was seen for the beech saplings. Some of this discussion appears in 4.3 – would it make sense to merge some of this?

Response: We agree with the reviewer that section 4.2 and 4.3 could be merged into one chapter summarizing all the drought responses and we thank him/her for this suggestion. We already tried to discuss the change in allocation strategy in the context of other studies in section 4.2. and 4.3 (Ruehr et al., 2009; Sanaullah et al., 2012; Bahn et al., 2013), but nevertheless we further improved this part of the manuscript as

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suggested by the reviewer.

Referee: Section 4.3. A puzzle seems to emerge in that belowground allocation of fresh assimilate was similar in control and drought plots whereas respiration of fresh assimilate was lower in the drought plots. By what mechanism would you speculate plants are able to influence this reduction in soil-respired fresh assimilate? Does it imply that grasses have a sort of valve controlling how much fresh assimilate is delivered to fungal symbionts and bacteria close to roots that consume exudate as opposed to its own root production?

Response: As shown by our data and now even more strongly, there is a trend towards a proportional higher allocation of fresh assimilates below-ground in drought plots for both years (see "Changes_Fig4.pdf), but a lower use of fresh assimilates in overall soil CO₂ efflux. This shows that proportionally more fresh assimilates are incorporated into root growth (as below-ground biomass under drought conditions also increased, see above), likely to increase the possibility of plants foraging for water. Thus, less assimilates might be available for root exudates. In addition, as an effect of drought, microbial respiration is likely to be reduced as well, resulting in a lower soil CO₂ efflux. The latter had been shown earlier by Ruehr et al. (2009) and Barthel et al. (2011). Thus, drought seemed to reduce the direct coupling of photosynthesis and soil CO₂ efflux as it had been shown before for clipping or shading (Craine et al., 1998; Wan and Luo, 2003; Bahn et al., 2009). Thus, root growth, tracer recovery in root biomass and soil CO₂ efflux supported the second avenue of reasoning for our hypothesis, i.e., higher relative below-ground allocation of recent assimilates for root growth.

Referee: Fig 4. The letters indicating results of multiple comparison do not appear to be consistent with the stars indicating significance. How can the significance level be $p \leq 0.01$ while the letters are a and ab for example for shoots ¹³C excess at nighttime on day 0? With only two groups (control vs. treatment), how can you have a and ab? I would have expected only a and a or a and b to be used.

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Response: The stars show significant differences between control and treatment samples (comparison between control and drought treatment). The letters, on the other hand, show results from the Tukey HSD test where we compared samples within a group (within the control treatment and within the drought treatment) in order to investigate whether the ^{13}C excess changed over time. We changed the figure caption to make this clearer.

Former caption: “ ^{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 Recoveryroots 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.”

Adapted caption: “ ^{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). Filled symbols: control plots; open symbols: treatment plots (mean \pm 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: Samples with the same letter show no significant difference within the treatment group.”

Referee: Minor Corrections: Fig 3: treatment symbols do not appear as grey in my copy but rather as open (unfilled or white) circles. consider modifying the figure label to match.

Response: We changed the figure caption to “filled” and “open” symbols.

Referee: Table 2. SE is given in parentheses not brackets.

Response: We are not sure we understand this comment. Parentheses (or outside

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of the US: round brackets; <http://grammarist.com/grammar/parentheses/>) are identical signs, the terms seem to differ between British and American English. We checked with other BG papers and both terms are used (e.g., Imer et al. (2013) used “brackets”, while Brüggemann et al. (2011) used “parentheses” for (...)).

On behalf of all authors, sincerely,

Susanne Burri

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Below-ground biomass at Chamau 2011

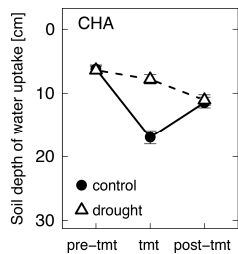
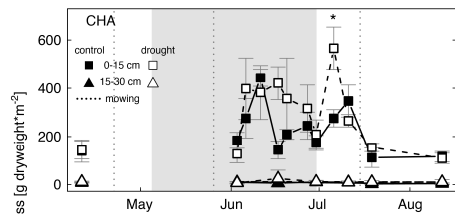


Fig. 1. Below-ground biomass

Former Table 2

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). ^ap ≤ 0.01 denotes significance level.

	Above-ground biomass			Below-ground biomass		
	Cut	Interpol.	Cut	Sampled	Interpol.	Sampled
2010						
Date	01 July	22 July	25 August	21 July	22 July	30 July
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	26 May	10 June	15 July	06 June	10 June	11 June
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

Fig. 2. Former Table2

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Adapted Table 2

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 ($n=3$). Letters denote significant differences between control and treatment (^a $p \leq 0.01$, ^b $p \leq 0.05$)

	Above-ground biomass			Below-ground biomass		
	Cut Date	Interpol. Date	Cut Date	Sampled Date	Interpol. Date	Sampled Date
2010	01 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	26 May	10 June	15 July	06 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

Fig. 3. Adapted Table 2

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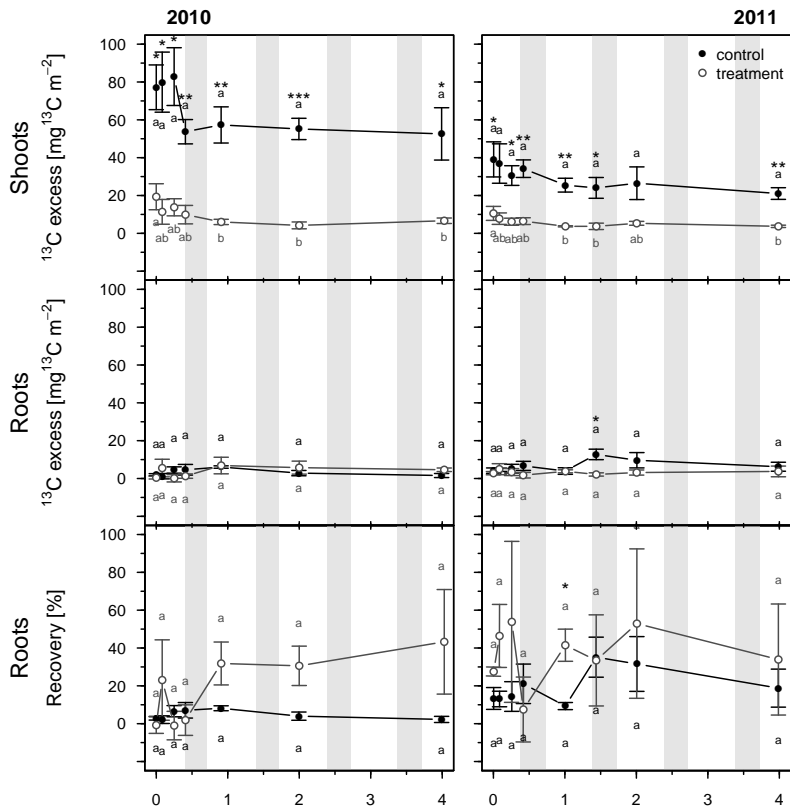


Fig. 4. Changes_Fig4

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