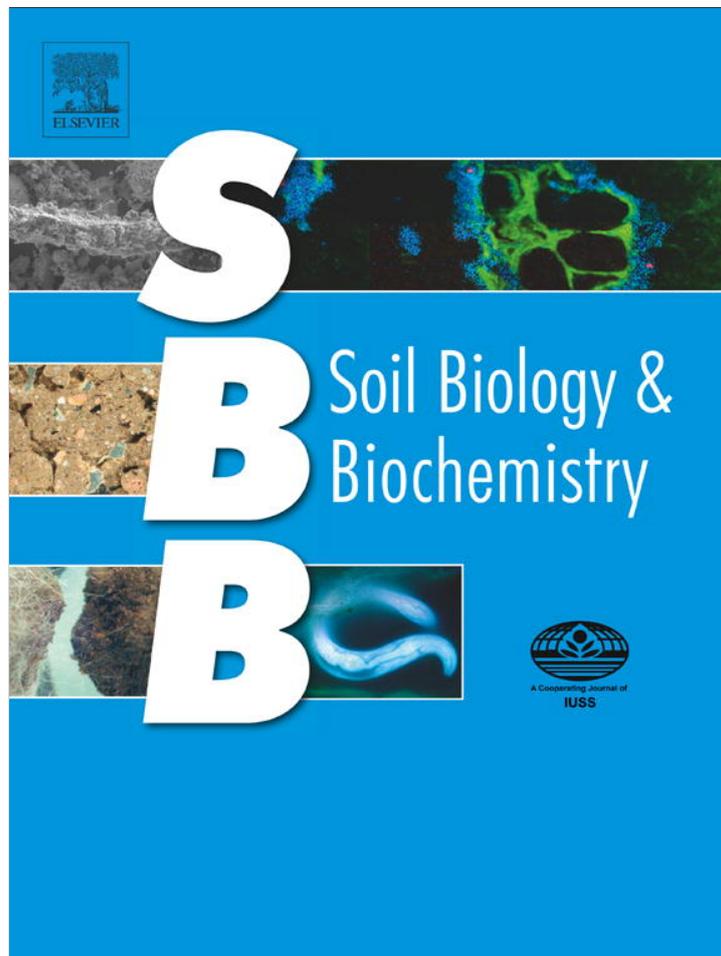


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Short communication

Drought-induced reduction in uptake of recently photosynthesized carbon by springtails and mites in alpine grassland

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ABSTRACT

We tested whether experimental summer drought affects the transfer of recently photosynthesized carbon from plants to soil mesofauna in a subalpine meadow. From day one after ¹³CO₂ pulse-labelling of the plant canopy, roots, collembolans and mites were enriched in δ¹³C in control, but not in drought plots. However, as the difference in δ¹³C between roots and soil animals was not affected by the drought treatment, we conclude that drought affects the tight linkage between photosynthesis and soil mesofauna primarily via functional responses of plants rather than via changes in the mesofauna.

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In the last decade extensive research on the response of various ecosystem compartments such as plants and aboveground fauna to global change has been conducted (Blankinship et al., 2011). Comparably few studies, however, have focused on the animals living belowground, despite their importance for biogeochemical cycling (Fierer et al., 2009). In a meta-analysis of effects of global change on soil biota, Blankinship et al. (2011) point out that soil animals are generally limited by water availability and that changes in precipitation may affect them more strongly than elevated CO₂ or warming. The suggested increase in the occurrence of drought episodes and heat waves in large parts of Europe (Meehl et al., 2007) may thus result in pronounced changes in soil fauna activity and community composition, with consequences on ecosystem functioning, including carbon dynamics (Bradford et al., 2007; Lindberg and Bengtsson, 2005; Van der Putten et al., 2009; Gavazov, 2010). It has been shown that invertebrates, such as collembolans and mites, may play an important role for carbon cycling by assimilating recent, photosynthetically fixed carbon and altering plant carbon inputs to the soil (Johnson et al., 2005; Ostle et al., 2007). However, little is known if and how

drought affects the flow of recent photoassimilates through these microarthropods.

Drought reduces photosynthesis and thus potentially also the supply of recent C belowground (Larcher, 2003; Schwalm et al., 2010). Furthermore, reductions in soil moisture likely reduce the activity of the mesofauna (Gavazov, 2010). Therefore, we hypothesize that the uptake of recently assimilated C by soil mesofauna is reduced by summer drought. To test this hypothesis, a ¹³CO₂ pulse labelling experiment was conducted, tracing effects of experimental summer drought on the uptake of recent C by collembolans and mites occurring in a subalpine meadow. This experiment was part of a larger study investigating how summer drought affects carbon allocation and respiratory use in the plant–soil system of mountainous grasslands.

The experiment was conducted on a subalpine meadow at 1850 m a.s.l. in the Austrian Central Alps (see Appendix S1). Three plots from which precipitation had been excluded for 5 weeks and three control plots (for details see Appendix S1) were pulse-labelled in the center (1 × 1 m) for 90 min with 99.9 atom% ¹³CO₂ as described in Bahn et al. (2009). At the time of sampling, soil moisture in the control plots and the drought plots was in the range of 25–35% vol. and 5–10% vol., respectively. In each plot two soil samples (∅ 5 cm, depth 5 cm; in PVC-tubes) were taken before and 1, 2 and 4 days after the ¹³CO₂ label was applied. Over a period of 10

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days the mesofauna was extracted from these samples in a Berlese apparatus using salt water as collection fluid. The extracted invertebrates were retrieved after 5 and 10 days to avoid their decay. Mites were identified to suborders, representing a rough classification of feeding guilds. For stable isotope analysis animals were dried at 70 °C overnight and weighed into tin capsules. Due to low numbers and the small size of the invertebrates, specimens from the two samples per plot and time point had to be pooled to obtain the minimum mass of 0.1 mg for analysis. Carbon stable isotopes were analyzed with an elemental analyzer coupled to an isotope ratio mass spectrometer (Thermo Scientific). Data was analyzed by ANOVA using R (R Development Core Team, 2010).

The drought treatment, which caused soil moisture to decline to less than 15% vol. as compared to 35–50% vol. in control plots, did not cause a significant decline in abundances of microarthropods (Appendix S3 and Table S1). However, drought had a significant effect on isotope values of both roots and soil animals. From the first day after labelling, a pronounced increase in $\delta^{13}\text{C}$ values of roots and microarthropods was observed in control plots, but not in drought plots (Fig. 1). Differences between control and drought plots were significant for collembolans ($F_{1,21} = 7.35$, $p = 0.013$) and mites ($F_{1,39} = 10.91$, $p = 0.002$). Collembolans were significantly more enriched in $\delta^{13}\text{C}$ than mites in the respective treatments ($F_{3,60} = 10.84$, $p < 0.001$). Furthermore, label incorporation in the control plots increased until day 4 for collembolans, being significant on day 2 (Fig. 1). For mites, the signal significantly increased already after one day, but decreased on day 4. Notably, the differences in $\delta^{13}\text{C}$ between roots and soil animals were similar in both

control and drought plots ($F_{3,60} = 0.337$, $p = 0.799$). Four days after labelling the difference in $\delta^{13}\text{C}$ values between roots and collembolans was 14.4‰ (SD = 16.7) in control and 10.2‰ (SD = 8.6) in drought plots, differences between roots and mites were 26.5‰ (SD = 18.0) and 20.8‰ (SD = 4.0), respectively.

Our data confirm a recently suggested strong and rapid link between living plants and the soil mesofauna (Ostle et al., 2007). Although grassland soil food webs are considered to be detrital-based systems, a significant amount of recent, photosynthetically fixed carbon enters the soil food web. Collembolans may affect the carbon-cycle via the mycorrhizosphere by either feeding on or incidentally damaging hyphae (Johnson et al., 2005), but have also been shown to function as herbivores in the presence of plant roots (Endlweber et al., 2009). Mites, here including representatives of the orders Oribatidae, Actinididae and Gamasidae, comprise detritivores, predators, and herbivores. Pooling these feeding guilds obviously resulted in lower $\delta^{13}\text{C}$ values compared to collembolans. Nonetheless, recent carbon was detected in this order, suggesting that herbivory might be found in this group.

In support of our hypothesis, drought significantly decreased the amount of recently photosynthesized carbon in the soil animals' tissues. As the difference in $\delta^{13}\text{C}$ between roots and soil animals was not significantly affected by the drought treatment, we conclude that drought did not affect the activity and the feeding behaviour of these two mesofauna groups *per se*. As photosynthetic activity of plants is constrained (Larcher, 2003; Schwalm et al., 2010) and C allocation is altered under drought (Brüggemann et al., 2011), less recent carbon enters the belowground plant

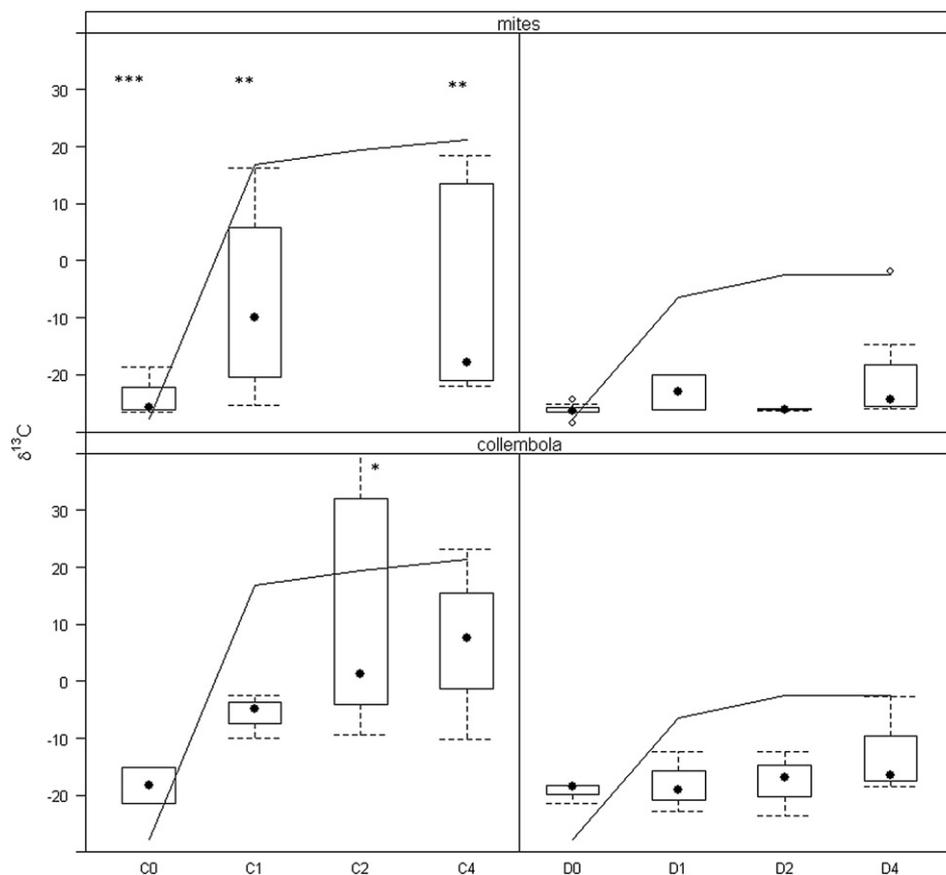


Fig. 1. Carbon isotope composition of mites (boxplots, upper panel), collembolans (boxplots, lower panel) and roots (lines, standard deviations are in the range of 12–24 permil) after ^{13}C pulse-labelling of control (C) and drought (D) plots in a subalpine meadow. Numbers indicates sampling time (0...before pulse labelling, 1,2,4...days after pulse labelling). Asterisks indicate significant differences between sampling times (* 0.05, ** 0.01, *** 0.001). Note that the missing value in C3 for mites is due to unsuccessful extraction of any mites for this sampling date.

system, which results in lower $\delta^{13}\text{C}$ values of soil animals. We therefore conclude that drought affects the tight linkage between photosynthesis and soil mesofauna primarily via functional responses of plants rather than of the mesofauna soil food web.

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Appendix A. Supplementary material

Supplementary data related to this article can be found online at <http://dx.doi.org/10.1016/j.soilbio.2012.06.009>.

References

- Bahn, M., Schmitt, M., Siegwolf, R., Richter, A., Brüggemann, N., 2009. Does photosynthesis affect grassland soil-respired CO_2 and its carbon isotope composition on a diurnal timescale? *New Phytologist* 182, 451–460.
- Blankinship, J.C., Niklaus, P.A., Hungate, B.A., 2011. A meta-analysis of responses of soil biota to global change. *Oecologia* 165, 552–565.
- Bradford, M.A., Tordoff, G.M., Black, H.I.J., et al., 2007. Carbon dynamics in a model grassland with functionally different soil communities. *Functional Ecology* 21, 690–697.
- Brüggemann, N., Gessler, A., Kayler, Z., Keel, S.G., Badeck, F., Barthel, M., Boeckx, P., Buchmann, N., Brugnoli, E., Esperschütz, J., Gavrichkova, O., Ghashghaie, J., Gomez-Casanovas, N., Keitel, C., Knohl, A., Kuptz, D., Palacio, S., Salmon, Y., Uchida, Y., Bahn, M., 2011. Carbon allocation and carbon isotope fluxes in the plant–soil–atmosphere continuum: a review. *Biogeosciences* 8, 3457–3489.
- Endlweber, K., Ruess, L., Scheu, S., 2009. Collembola switch diet in presence of plant roots thereby functioning as herbivores. *Soil Biology and Biochemistry* 41, 1151–1154.
- Fierer, N., Strickland, M.S., Liptzin, D., Bradford, M.A., Cleveland, C.C., 2009. Global patterns in belowground communities. *Ecology Letters* 12, 1238–1249.
- Gavazov, K.S., 2010. Dynamics of alpine plant litter decomposition in a changing climate. *Plant and Soil* 337, 19–32.
- Johnson, D., Krsek, M., Wellington, E.M.H., Stott, A.W., Cole, L., Bardgett, R.D., Read, D.J., Leake, J.R., 2005. Soil invertebrates disrupt carbon flow through fungal networks. *Science* 309, 1047.
- Larcher, W., 2003. *Physiological Plant Ecology*, fourth ed. Springer, 513 pp.
- Lindberg, N., Bengtsson, J., 2005. Population responses of oribatid mites and collembolans after drought. *Applied Soil Ecology* 28, 163–174.
- Meehl, G.A., Stocker, C.M., Bowker, T.F., Collins, C.M., Bowker, W.D., Friedlingstein, C.M., Bowker, P., Gaye, C.M., Bowker, A.T., Gregory, C.M., Bowker, J.M., et al., 2007. Global climate projections. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), *Climate Change 2007: the Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Ostle, N., Briones, M.J.I., Ineson, P., Cole, L., Staddon, P., Sleep, D., 2007. Isotopic detection of recent photosynthate carbon flow into grassland rhizosphere fauna. *Soil Biology and Biochemistry* 39, 768–777.
- R Development Core Team, 2010. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0. URL: <http://www.R-project.org/>.
- Schwalm, C.R., Williams, C.A., Schaefer, K., Arneith, A., Bonal, D., Buchmann, N., Chen, J., Law, B.E., Lindroth, A., Luyssaert, S., Reichstein, M., Richardson, A.D., 2010. Assimilation exceeds respiration sensitivity to drought: a FLUXNET synthesis. *Global Change Biology* 16, 657–670.
- Van der Putten, W.H., Bardgett, R.D., de Ruiter, P.C., et al., 2009. Empirical and theoretical challenges in aboveground–belowground ecology. *Oecologia* 161, 1–14.