



Incorporation of root-derived carbon into soil microarthropods varies between cropping systems

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Abstract

As the dynamics and magnitude of rhizodeposition vary considerably among cropping systems, we investigated effects of cropping system on the incorporation of root-derived carbon (C) into Collembola, a dominant taxon of soil microarthropods. In the field, we used ¹³CO₂ to pulse label a crop monoculture (oilseed rape, *Brassica napus* L.), a mixed-grass community (dominated by *Lolium perenne* L. mixed with clover *Trifolium repens* L.), and a tree plantation (willow, *Salix schwerinii* E.L. Wolf and *Salix viminalis* L.). During 28 days, the incorporation of ¹³C was traced in nine species of Collembola including epedaphic (surface-dwelling), hemiedaphic (litter-dwelling), and euedaphic (soil-dwelling) functional groups. Incorporation of ¹³C into Collembola reached a plateau before day 3 after the labeling in grass and willow, but increased up to day 14 in rape. While euedaphic Collembola incorporated less root-derived C than epedaphic and hemiedaphic Collembola in rape and willow, the incorporation of ¹³C was similar among functional groups in grass. Differential incorporation of ¹³C in euedaphic species points to niche differentiation within the same functional group. Our findings highlight that cropping system not only affects the flux of root C into soil mesofauna, being slower in rape than in grass and willow, but also the utilization of root-derived resources by functional groups and species of Collembola. The results indicate that pronounced differences in belowground C inputs between cropping systems affect microbivores as basal species and thereby soil food webs and their functioning and services.

Keywords ¹³C labeling · Collembola · Functional group · Grass · Rape · Willow

Introduction

Considerable amounts (10–20%) of C are released by plants into soil as rhizodeposition shortly after fixation (Kuzzyakov and Domanski 2000; Dennis et al. 2010). This root-derived C

comprises mainly low-molecular-weight compounds, such as glucose, organic acids, and amino acids, which are preferentially taken up by soil organisms (Dennis et al. 2010). Collembola play a major role in soil food webs, contributing to C transport at the litter-soil interface (Chamberlain et al.

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2006), and channeling C and nutrients from multiple resources to predators at higher trophic levels (Oelbermann et al. 2008; Liu et al. 2016). Stable isotope studies showed that Collembola quickly incorporate recently fixed C via multiple pathways, including plants, bacteria, saprotrophic/mycorrhizal fungi, and other soil animals (Pollierer et al. 2012; Ferlian et al. 2015; Scheunemann et al. 2016). However, how cropping systems affect the incorporation of root-derived C into Collembola is little understood.

Incorporation of root C into the soil food web depends on the allocation of recently fixed C by plants to roots and rhizodeposits, and this varies with the strategies of plants to exploit nutrients from soil (Kuzyakov and Domanski 2000; Pausch and Kuzyakov 2018). Crops allocate large amounts of fixed C to aboveground biomass since they typically are selected to maximize the growth of fruits and grains, leading to low flux of fixed C to belowground plant compartments (Pausch and Kuzyakov 2018). The application of fertilizers also results in low allocation of assimilates to belowground plant compartments due to decreasing plant investment in nutrient absorption (Phillips et al. 2011). By contrast, grass and trees are likely to allocate more fixed C below the ground as compared to annual crops, as they invest more into the exploitation of nutrients from soil (Grayston et al. 1997; Pausch and Kuzyakov 2018). In addition, rhizosphere microorganisms differ between cropping systems; for example, mycorrhizal fungi effectively distribute recently fixed plant C to the soil microbial community and may facilitate the uptake of root-derived C by microbivores.

Different functional groups of Collembola living in different soil depths potentially differ in the utilization of root-derived C (Potapov et al. 2016a). Due to closer association with roots, euedaphic Collembola inhabiting the mineral soil presumably incorporate more root-derived C than hemiedaphic and epedaphic Collembola, which preferentially colonize organic layers or the soil surface (Scheunemann et al. 2010; Potapov et al. 2016a). However, incorporation of root-derived C by different functional groups may differ between cropping systems due to trophic plasticity of Collembola species (Ruess et al. 2005; Endlweber et al. 2009; Scheunemann et al. 2015; Eerpina et al. 2017).

To explore variations in the incorporation of plant-derived C into Collembola, we pulse labeled three cropping systems with ^{13}C and traced the incorporation of root C into nine Collembola species of different functional groups. The cropping systems included a herbaceous crop monoculture (oilseed rape, *Brassica napus* L.), a mixed-grass community (grassland dominated by *Lolium perenne* L. mixed with clover *Trifolium repens* L.), and a tree plantation (willow, *Salix schwerinii* E.L. Wolf and *Salix viminalis* L.). We tested the following hypotheses: (i) The incorporation of root C from grass and willow into Collembola is faster than that from rape, due to higher belowground C allocation in grasses and trees

than in annual crops, and/or to application of fertilizer and lack of mycorrhizal symbiosis in rape. (ii) Euedaphic Collembola incorporate more root-derived C than epedaphic and hemiedaphic Collembola due to closer association of euedaphic Collembola with plant roots. (iii) Incorporation of root-derived C differs between species within functional groups and the differences will vary among cropping systems.

Materials and methods

Site description

The study sites were located in Reiffenhausen, south of Göttingen in central Germany (51° 39' 83" N/9° 98' 75" E; 325 m.a.s.l.). Average annual temperature is 9.1 °C, and the mean annual precipitation is 635 mm (Richter et al. 2015). The soil at the study sites is sedimentary deposits of Middle and Upper Triassic Sandstone material, partly mixed with claystone material and covered by loess sediments. The texture of soil varies from loamy sand in the eastern part to silty loam in the western part (Hartmann and Lamersdorf 2015; Tariq et al. 2018). The experiment was established on former cropland in March 2011. The preceding crop grown on the experimental sites was winter barley (*Hordeum vulgare* L.).

Experimental design

Fields planted with three cropping systems comprising rape (oilseed rape, *Brassica napus* L.), grass (dominated by *Lolium perenne* L., mixed with clover *Trifolium repens* L.), and tree (willow, *Salix schwerinii* E.L. Wolf and *Salix viminalis* L.) were established (Ehret et al. 2015; Tariq et al. 2018). The willow and grass sites were established in March 2011. In September 2015, part of the grass sites was transformed into rape fields. The rape site represents cropland of high land-use intensity including fertilizer application, annual harvest, and crop rotation. The grass site represents low input grassland without fertilizer application but with three cuts per year (Ehret et al. 2015). The willow site was planted as low input short-term forest rotation system with a rotation cycle of 3 years without application of fertilizer. The willow trees were about 3 years old and 4 m height in our experiment. The willow site and grass site were arranged as an agroforest with rows of willow stripes and grassland strips in between (three willow stripes, each 7.5 m wide and 75 m long, and three grassland stripes, each 9 m wide and 75 m long). The rape site was next to one of the outer willow stripes (18 m wide and 75 m long).

In each of cropping systems, five labeling chambers were installed. In the rape field, the chambers were randomly positioned at a distance of 5 to 10 m from each other in May 2017. For labeling willow, one stripe adjacent to the rape field was

selected and the chambers were spaced at least by 10 m and installed in July 2017. In the grass stripes, grass plots were established as blocks differing in, e.g., application of fertilizer (Ehret et al. 2015). Since the size of individual blocks (9.0×6.5 m) was too small to install five chambers, we installed the chambers in two blocks with the same treatment (no fertilizer addition) in August 2017, two chambers in block one which was next to the selected willow stripe, and three chambers in block two spaced by 50 m to block one. The chambers consisted of stainless steel frames of 1×1 m which were inserted into the soil to a depth of 10 cm and of a plastic frame on top (height 1 m for rape and grass, 2 m for willow) that was covered with translucent LDPE (low-density polyethylene) foil. Plants were labeled by the addition of HCl to 20 g $\text{Ca}^{13}\text{CO}_3$ in a plastic beaker. In willow, upper branches were bent to fit the height of the chamber. In addition, understory plants were removed and the soil surface was covered with black plastic foil before labeling to exclude ^{13}C incorporation by herbaceous plants and algae. The produced $^{13}\text{CO}_2$ was circulated in the chambers by a fan for 6 h. After labeling, the foil and plastic frame were removed, while the steel frame remained in the soil to prevent migration of animals between labeled and unlabeled areas (Scheunemann et al. 2016). The fact that ^{13}C enrichment did not decrease in most Collembola species throughout the experiment indicated that this procedure was effective.

Sites of different cropping systems were close to each other and were established on one former field. Therefore, our study sites may not be perfectly independent of each other. However, establishing the study sites on similar background provided a number of advantages for testing our hypothesis. First, small spatial distances between sites allowed us to sample the same Collembola species across all study sites, a crucial precondition to study variations in nutrition of Collembola species between cropping systems. In addition, it restricted effects of confounding variables, such as differences in soil type, on the flux of root C into soil food webs. Finally, the distance between labeling chambers was at least 5 m to minimize spatial dependence.

Sampling

Soil samples were taken 3, 7, 14, and 28 days after labeling to analyze the dynamics of ^{13}C incorporation into Collembola. Additionally, unlabeled samples were taken at adjacent plots and served as control for analyzing ^{13}C and ^{15}N natural abundance in each cropping system. In each chamber, one soil sample was taken at each sampling date using a stainless steel soil corer (diameter 20 cm, depth 10 cm). Soil arthropods were extracted by heat (Kempson et al. 1963) and stored in 70% ethanol at -20 °C. Collembola were identified to species level using a Zeiss microscope (Hopkin 2007). The nine abundant Collembola species across all sites were selected for stable

isotope analysis: epedaphic species including *Isotoma viridis* (Bourlet), *Lepidocyrtus cyaneus* (Tullberg), *Lepidocyrtus paradoxus* (Uzel), and *Orchesella villosa* (Geoffroy); hemiedaphic species including *Folsomia quadrioculata* (Tullberg), *Parisotoma notabilis* (Schäffer), and *Pseudosinella alba* (Packard); and euedaphic species including *Protaphorura armata* (Tullberg) and *Stenaphorura denisi* (Bagnall). The classification of functional groups was based on Potapov et al. (2016b).

Stable isotope analysis

Approximately 50 µg of dry weight of each Collembola species (from 1 to 30 individuals) was weighed into tin capsules, which were analyzed for $^{13}\text{C}/^{12}\text{C}$ with a coupled system of an elemental analyzer (NA1110, CE-Instruments, Rodano, Milano, Italy) and an isotope ratio mass spectrometer (Delta Plus, Finnigan MAT, Bremen, Germany) located at the Centre for Stable Isotope Research and Analysis, Göttingen, Germany. V-PDB was used as a standard for ^{13}C . Acetanilide was used for internal calibration. Isotope natural abundance was expressed using the delta notation with $\delta^{13}\text{C} = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}] \times 1000$. R_{sample} and R_{standard} refer to the $^{13}\text{C}/^{12}\text{C}$ in samples and standard, respectively. Incorporation of ^{13}C into Collembola was calculated for each species as shift in the isotope signature between labeled and control sample as ^{13}C enrichment $\Delta^{13}\text{C} [\text{‰}] = \delta^{13}\text{C}_{\text{labeled sample}} - \delta^{13}\text{C}_{\text{unlabeled sample}}$. Data on $\Delta^{13}\text{C}$ of shoot/leave and root (visible fine roots shorted by hand), soil dissolved organic C, and soil PLFAs were provided by Lingling Shi (unpubl. data).

Statistical analysis

$\Delta^{13}\text{C}$ values of Collembola were compared between sampling days, Collembola species, and functional groups using linear mixed effects models for each cropping system. In the first model, species and sampling days were set as fixed effects. As different spatial scales investigated were nested in a hierarchical structure (“soil core” nested within “chamber,” “chamber” nested within “cropping system”), stable isotope data of Collembola from the same soil core and from the same chamber were not independent. We accounted for this by setting “chamber” and “soil core” nested within “chamber” as random effects. In the second model, $\Delta^{13}\text{C}$ values of Collembola were compared between functional groups of Collembola and days with “species,” “chamber,” and “soil core” nested within “chamber” as random effects. In the third model, we averaged $\Delta^{13}\text{C}$ values from different sampling days for each chamber and species and used the natural abundance $\delta^{13}\text{C}$ values as fixed effects; random effects were “chamber” and “species.” Since chambers in grass were distributed in two blocks, we also used “block” as random effect in the model of grass.

Because the epedaphic species *L. paradoxus* had considerably lower $\Delta^{13}\text{C}$ values in rape and distinct dynamics compared to the other three epedaphic species, it was excluded in the second and third models. Similar to the third model, we also analyzed the relationship between average $\Delta^{13}\text{C}$ values of Collembola species and their body length and abundance in rape, grass, and willow.

For each model, heteroscedasticity was inspected by plotting the residuals against the predicted values and normality was checked by Quantile-Quantile plots. $\Delta^{13}\text{C}$ values were transformed (logarithmic or Box-cox transformations) if homogeneity of variance and normality were not satisfied. All statistical analyses were conducted using R 3.4.2 (R Core team 2016), packages *lme4* (Bates et al. 2015), and *lmerTest* (Kuznetsova et al. 2017). Plots were drawn in R using the package *ggplot2* (Wickham 2016).

Results

Incorporation of ^{13}C into Collembola in different cropping systems

Three days after labeling, the ^{13}C enrichment of shoots of rape, grass, and willow was 399.6 ± 91.7 , 826.6 ± 209.6 , and 355.1 ± 176.5 ‰, respectively (Table S1). High ^{13}C concentration in plant tissue early after labeling allowed us to reliably trace the incorporation of recently fixed C into Collembola.

The incorporation of ^{13}C into Collembola differed markedly between sampling days in rape, but stayed relatively constant in grass and willow (Table 1). Except for *L. paradoxus* and *S. denisi*, ^{13}C incorporation into Collembola in rape increased gradually after labeling, reached a plateau at day 7 or 14 and then stayed constant until day 28 (Fig. 1). In grass, ^{13}C incorporation was already high at day 3 and stayed relatively

constant in most species except for *L. paradoxus* and *O. villosa*, which reached their peaks at days 7 and 14, respectively (Fig. 2). In willow, ^{13}C incorporation (overall mean enrichment 13.6 ± 19.9 ‰) was generally lower than that in grass (187.3 ± 216 ‰) and rape (80.99 ± 74.8 ‰) and stayed more constant than that in rape after labeling. Incorporation of ^{13}C in willow was lowest in *S. denisi* and *P. armata* (Fig. 3).

Incorporation of ^{13}C into Collembola functional groups

Incorporation of ^{13}C differed significantly between Collembola functional groups in willow and rape, with epedaphic and hemiedaphic Collembola being more enriched than euedaphic Collembola (Table 2, Fig. 4). In rape, differences between functional groups depended on sampling day, being more pronounced after day 7. By contrast, incorporation of ^{13}C did not differ significantly between functional groups in grass (Table 2, Fig. 4).

Species-specific differences in the incorporation of ^{13}C

The random effects of species in the model of functional groups were significant in all cropping systems ($p < 0.001$); that is, the incorporation of ^{13}C into Collembola significantly differed between species within the same functional group (Table 1). In the euedaphic group, $\Delta^{13}\text{C}$ values in *P. armata* were significantly higher than those in *S. denisi* in each of the cropping systems (Fig. 5). Species-specific differences in the other functional groups depended on cropping system. For instance, *P. alba* was more enriched than the other hemiedaphic species in grass and willow, but not in rape. $\Delta^{13}\text{C}$ values in *L. paradoxus* were lower than those in the other epedaphic species in rape, but similar in grass and willow.

Table 1 Linear mixed effects model of type III error for the effect of species, sampling day, and their interaction on the incorporation of ^{13}C into Collembola in different cropping systems (rape, grass, and willow)

Cropping system	Factor	Sum of square	Mean of square	df1	df2	<i>F</i> value	<i>P</i> value
Rape	Species	22.09	2.76	8	97.22	<i>66.68</i>	< 0.001
	Day	9.83	3.28	3	13.07	<i>79.15</i>	< 0.001
	Species × day	4.54	0.19	24	96.97	<i>4.57</i>	< 0.001
Grass	Species	9.47	1.18	8	79.81	<i>23.70</i>	< 0.001
	Day	0.05	0.05	3	14.75	0.33	0.804
	Species × day	3.83	0.16	24	80.25	<i>3.19</i>	< 0.001
Willow	Species	7.02	0.88	8	73.85	<i>18.33</i>	< 0.001
	Day	0.47	0.16	3	15.13	3.25	0.052
	Species × day	1.19	0.05	24	74.93	1.03	0.439

df1 numerator degree of freedom, df2 denominator degree of freedom

Significant effects are in italics

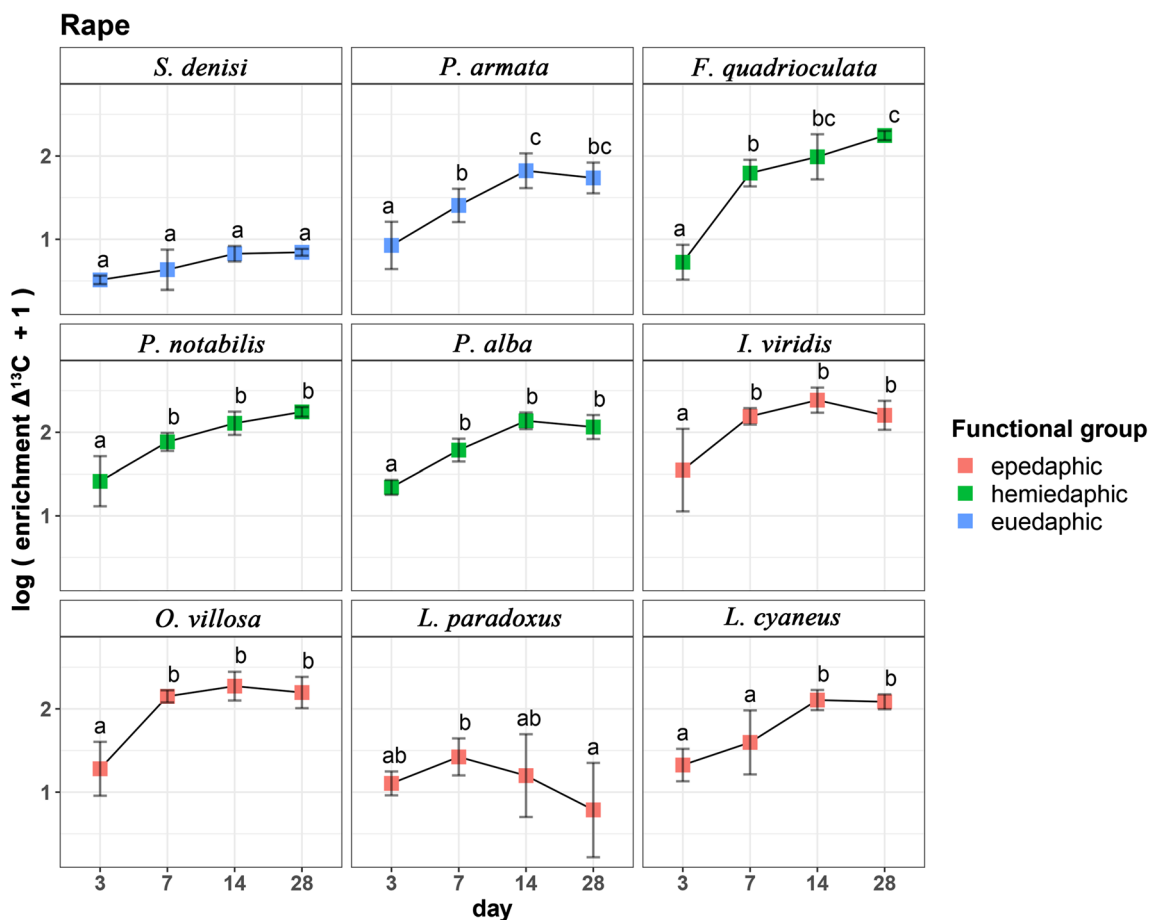


Fig. 1 Incorporation of ^{13}C into Collembola species (*Stenaphorura denisi*, *Protaphorura armata*, *Folsomia quadrioculata*, *Parisetoma notabilis*, *Pseudosinella alba*, *Isotoma viridis*, *Orchesella villosa*, *Lepidocyrtus paradoxus*, *Lepidocyrtus cyaneus*) 3, 7, 14, and 28 days

after labeling in rape; means \pm SD. Values of different sampling dates within a species with the same letters are not significantly different ($p < 0.05$; Tukey’s HSD test)

$\Delta^{13}\text{C}$ values of Collembola species negatively correlated with their natural abundance values of ^{13}C ($\delta^{13}\text{C}$) in rape, grass, and willow; however, the correlation was not significant in the latter (Table S2, Fig. 6). In none of the cropping systems, $\Delta^{13}\text{C}$ values of Collembola species were significantly correlated with their abundance nor their body length (data not shown).

Discussion

Influence of cropping system on the utilization of root C

Collembola rapidly incorporated the labeled C in each of the cropping systems (rape, grass, and willow), indicating that soil food webs under these cropping systems are fueled by recently fixed C. This is in line with previous studies showing that soil invertebrates incorporated recently fixed C in arable systems, grasslands, temperate, and boreal forests, most likely via rhizodeposits and associated microorganisms (Pollierer et al.

2007; Högberg et al. 2010; Seeber et al. 2012; Eissfeller et al. 2013; Goncharov et al. 2016; Scheunemann et al. 2016). Our study for the first time showed that incorporation dynamics of recently fixed C and its distribution among different functional groups and species of Collembola are markedly different among cropping systems.

Supporting our first hypothesis, the incorporation of ^{13}C into Collembola reached a peak on days 0–3 in grass and willow but at day 7 or 14 in rape (Figs. 1, 2, and 3), indicating slower root C flux into Collembola in rape than in grass and willow. In other labeling experiments, incorporation of ^{13}C into Collembola also increased with time in cropland (Pausch et al. 2016; Scheunemann et al. 2016), while staying relatively constant or without clear trend in grassland (Ostle et al. 2007) and forest (Högberg et al. 2010; Fujii et al. 2016). This may reflect the lower C allocation to roots in rape compared to grass and willow (Kuzyakov and Domanski 2000; Pausch and Kuzyakov 2018), presumably because crop species are selected to maximize the growth of harvested plant compartments (Pausch and Kuzyakov 2018). By contrast, perennial grasses translocate more C belowground (30–50%)

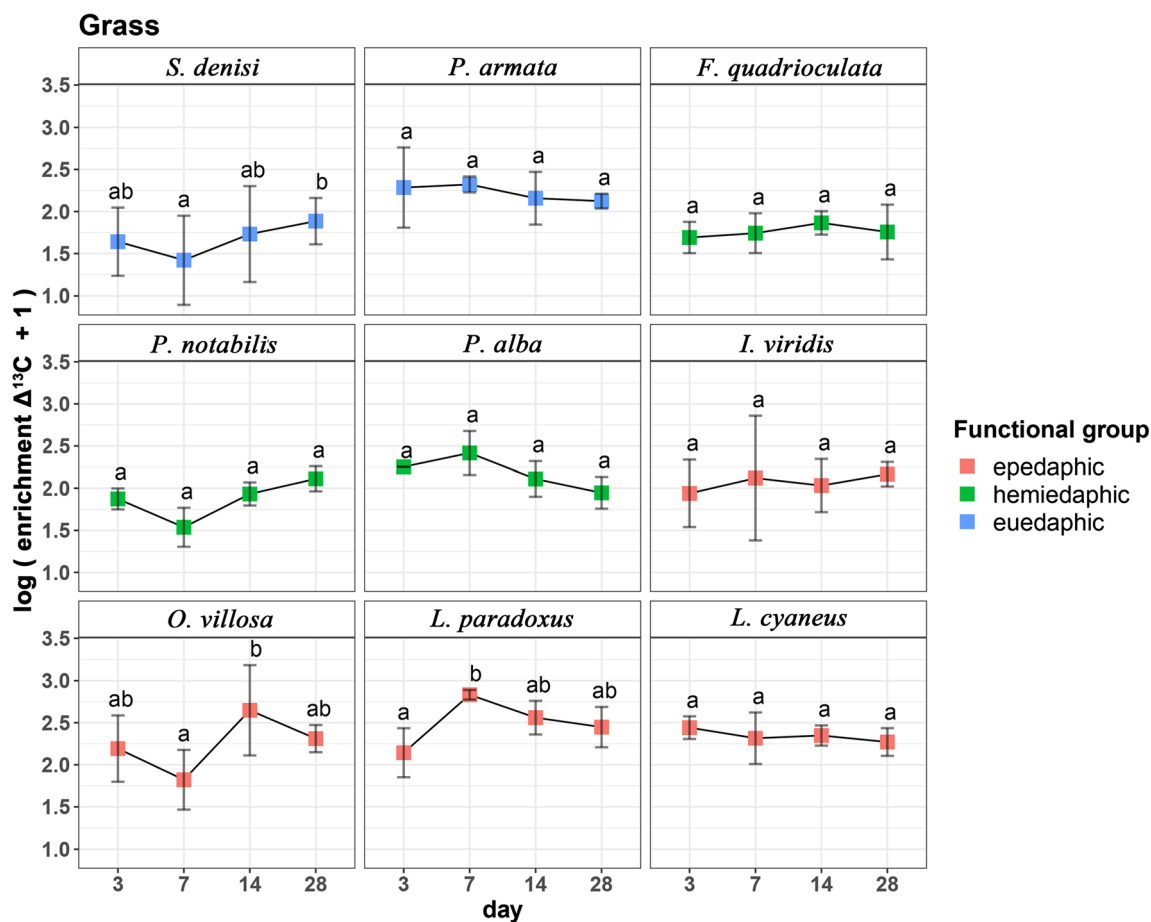


Fig. 2 Incorporation of ^{13}C into Collembola species 3, 7, 14, and 28 days after labeling in grass; means \pm SD. Values of different sampling dates within a species with the same letters are not significantly different ($p < 0.05$; Tukey's HSD test). For abbreviations, see Fig. 1

than crops (20–30%) since they rely on belowground C reserves for regrowth in spring and after grazing or mowing (Pausch and Kuzyakov 2018). Application of fertilizer likely further decreased belowground C allocation in rape. Typically, fertilization with N reduces the allocation of C to roots and the root-to-shoot biomass ratio (Hermans et al. 2006), which directly or indirectly results in lower C supply to soil microorganisms and animals (Ai et al. 2015; Deneff et al. 2009; Högberg et al. 2010). Supporting this assumption, the ^{13}C enrichment of dissolved organic C in soil increased gradually and peaked at day 14 in rape, while it peaked at day 3 in grass and willow (Table S3), reflecting lower exudation and/or lower microbial assimilation efficiency of root exudates in rape than in grass and willow. Thus, the transfer efficiency of root-derived C to microorganisms and to microbivorous arthropods presumably was lower in rape than in grass and willow.

Association between plants and soil microorganisms differs between cropping systems, and this is likely to be another important factor affecting the flux of root C into rhizosphere animal consumers such as Collembola. Grasses and willows form symbiotic associations with mycorrhizal fungi (Sumorok and Kiedrzyńska 2007; Baum et al. 2009; Nicolson and

Johnston 2009), and this might be associated with higher root exudation compared to non-mycorrhizal plants such as oilseed rape (Okubo et al. 2016). High allocation of plant C to mycorrhizal fungi and root exudates assimilated by saprotrophic rhizosphere microorganisms in grass and willow (Deneff et al. 2007; Kušliene et al. 2014) is likely to result in fast incorporation of root C into rhizosphere consumers. In addition, mycorrhizal and saprotrophic fungal mycelia efficiently transfer root C from the rhizosphere to root-free bulk soil (Butler et al. 2003; Kušliene et al. 2014) facilitating the capture of root C by Collembola. By contrast, incorporation of root C into animal consumers may be hampered by the absence of mycorrhizal associations in rape (Kühn et al. 2019). This likely results in a more uneven distribution of root C in bulk soil, thus reducing the incorporation of root-derived C into Collembola.

The ^{13}C incorporation into Collembola species was remarkably lower in willow than in grass and rape. Potentially, low enrichment in willow was due to high amounts of unlabeled C in the phloem that diluted the signal of ^{13}C , leading to lower $\Delta^{13}\text{C}$ values in Collembola even when incorporating similar amounts of root C as in grass and rape. Supporting this assumption, the ^{13}C enrichment of roots (Table S1) and of the

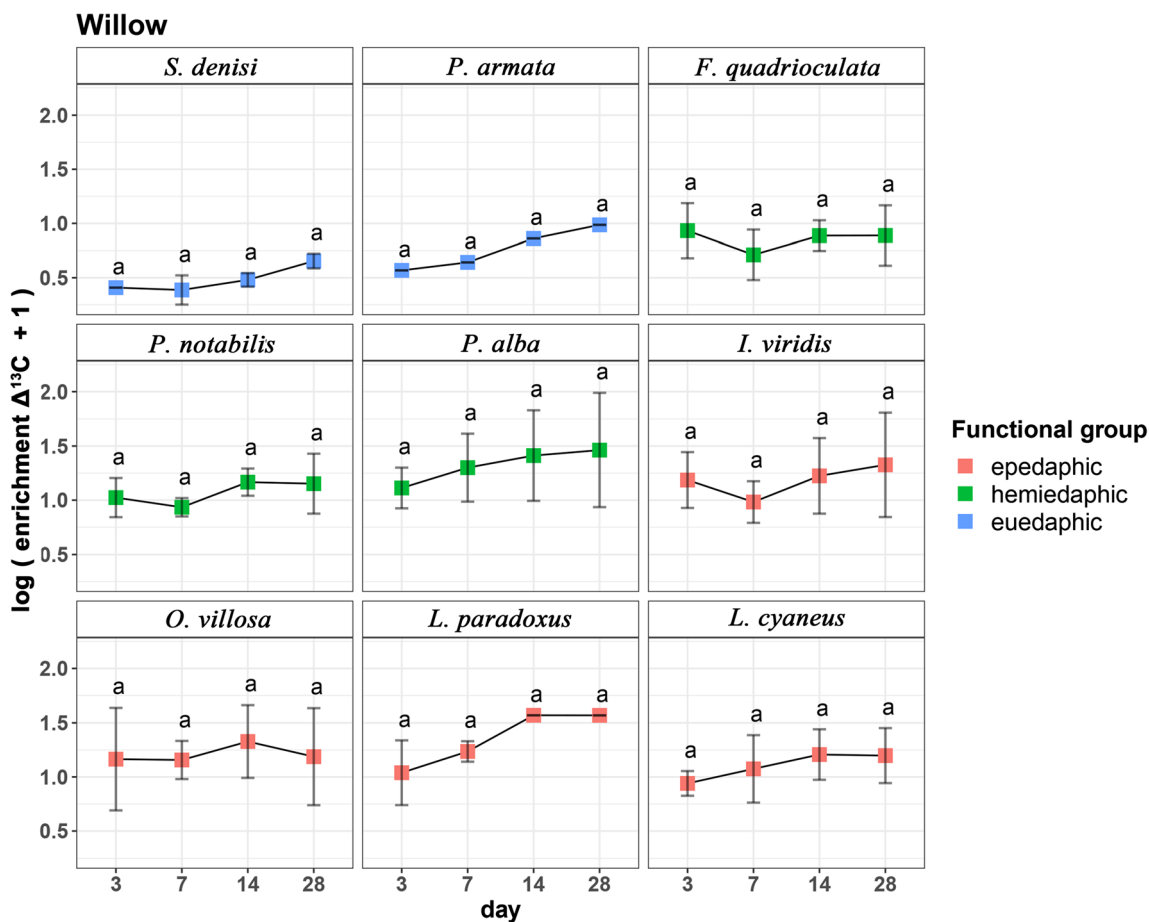


Fig. 3 Incorporation of ¹³C into Collembola species 3, 7, 14, and 28 days after labeling in willow; means ± SD. Values of different sampling dates within a species with the same letters are not significantly different (*p* < 0.05; Tukey’s HSD test). For abbreviations, see Fig. 1

biomarker PLFA 18:2ω6,9 in soil were also lower in willow than in grass and rape (Lingling Shi, unpubl. data). Although the PLFA 18:2ω6,9 originates from both roots and fungi, its close correlation with other fungal biomarkers (Högberg 2006; Pausch et al. 2016) and the fact that only sieved soil

was analyzed in the present study suggest that it predominantly reflects fungal tissue. Besides dilution effects, ¹³C loss via respiration of aboveground parts or low belowground allocation of recent photosynthate C may also have contributed to the low ¹³C incorporation into Collembola in willow.

Table 2 Linear mixed effects model table of type III error for the effect of functional group, sampling day, and their interaction on the incorporation of ¹³C into Collembola in different cropping systems (rape, grass, and willow)

Cropping system	Factor	Sum of square	Mean of square	df1	df2	<i>F</i> value	<i>P</i> value
Rape	fg	0.64	0.32	2	5.01	<i>6.60</i>	<i>0.039</i>
	Day	13.58	4.53	3	14.05	<i>94.06</i>	<i>< 0.001</i>
	fg × day	0.68	0.11	6	105.42	<i>2.34</i>	<i>0.036</i>
Grass	fg	0.28	0.14	2	5.85	1.87	0.235
	Day	0.13	0.04	3	15.79	0.59	0.634
	fg × day	0.42	0.07	6	98.76	0.93	0.481
Willow	fg	1.38	0.66	2	5.90	<i>6.62</i>	<i>0.031</i>
	Day	1.21	0.40	3	19.58	<i>4.01</i>	<i>0.022</i>
	fg × day	0.77	0.13	6	96.91	1.27	0.276

df1 numerator degree of freedom, *df2* denominator degree of freedom, *fg* functional group
Significant effects are in italics

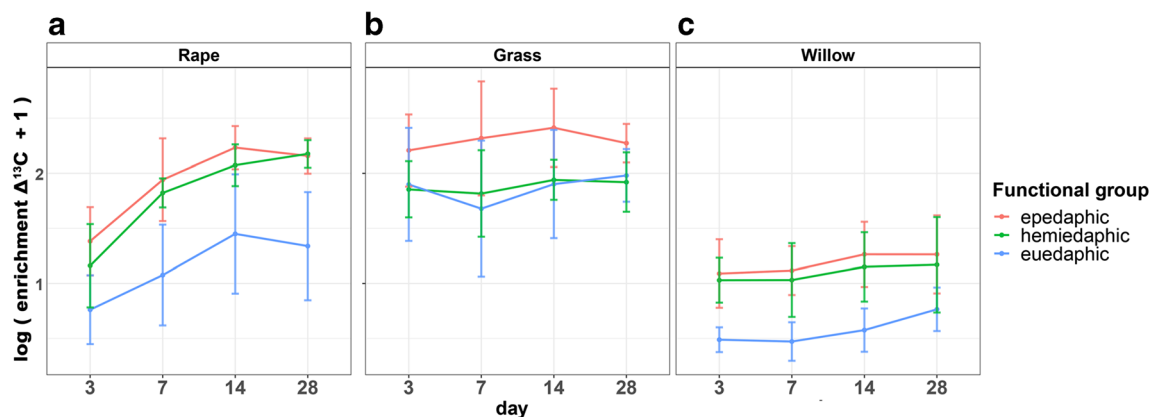


Fig. 4 Incorporation of ^{13}C into Collembola functional groups 3, 7, 14, and 28 days after labeling in fields planted with **a** rape, **b** grass, and **c** willow; means \pm SD

Unlike the sites of grass and willow, which were established directly from crop fields, the rape site was established from part of the grass site. Differences in preceding vegetation may have influenced the incorporation of root-derived C into Collembola due to differentially affecting soil properties and microbial communities. However, legacy effects of the preceding vegetation presumably were minor compared to effects of the present plant types/species and soil management. For instance, Detheridge et al. (2016) showed that the fungal community of cereal fields with different preceding crop species converged already 1 year after establishment. Similarly, Crotty et al. (2016) found that the legacy effect of preceding crop species on the diversity and abundance of soil fauna diminished in the second cropping season during crop rotation, and the abundance of Collembola did not vary any more with the previous crop species.

In the present study, we could not capture variation in belowground C allocation as influenced by growth period. As our study was conducted during the late growth period of oilseed rape, the rapid growth of flowers and seeds likely

diminished the flux of C to roots and into the soil food web, whereas belowground C allocation and incorporation presumably is higher in rape at early growth stages (Pausch and Kuzyakov 2018). In grasses, the variation in C allocation with growth stage is relatively minor as compared to annual crops (Pausch and Kuzyakov 2018), whereas the belowground C input from trees potentially is higher in the late than in the early growth period (Mordacq et al. 1986; Kagawa et al. 2006; Högberg et al. 2010). As patterns of ^{13}C incorporation into Collembola potentially differ between growth periods, in particular in rape and willow, further research on seasonal variation in belowground C inputs in different cropping systems is needed.

Incorporation of root C into Collembola functional groups

Functional groups of Collembola reflect the habitat they live in, such as litter, humus, and mineral soil (Faber 1991; Ponge 2000; Rusek 2007), which allows to infer distribution of root-

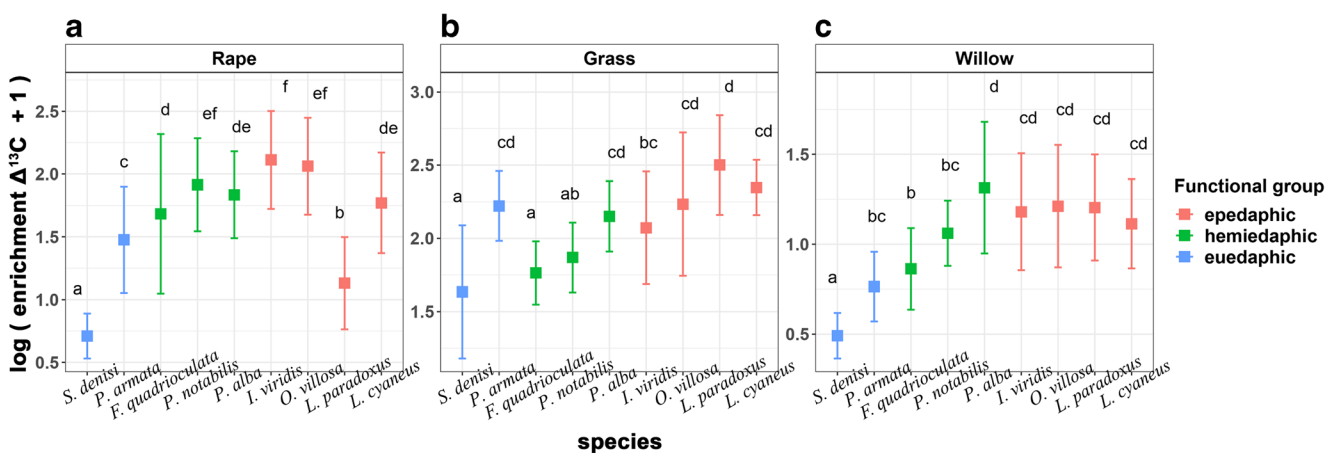


Fig. 5 Incorporation of ^{13}C into Collembola species in fields planted with **a** rape, **b** grass, and **c** willow; means \pm SD. All sampling dates are bulked together. Values of different species within a cropping system with the

same letters are not significantly different ($p < 0.05$; Tukey's HSD test). For abbreviations, see Fig. 1

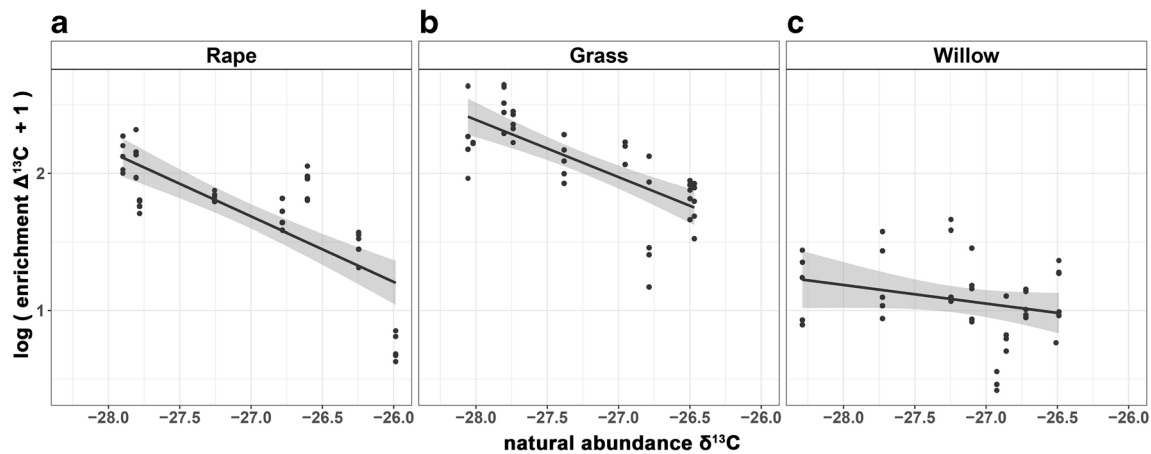


Fig. 6 Correlation between the incorporation of ^{13}C ($\Delta^{13}\text{C}$) and the natural abundance of ^{13}C ($\delta^{13}\text{C}$) of the same Collembola species in fields planted with **a** rape, **b** grass, and **c** willow; data are means per species and chamber

derived C in soil food webs at different soil depths (Potapov et al. 2016b). In contrast to our second hypothesis, hemiedaphic and epedaphic Collembola incorporated more ^{13}C than euedaphic Collembola in rape and willow (Fig. 4), indicating that soil-dwelling species have limited access to recently fixed C in these cropping systems. This contradicts previous findings in forests where hemiedaphic Collembola were not strongly labeled (Potapov et al. 2016a; Fujii et al. 2016), possibly because they relied on litter as the major C source in these systems. By contrast, our studies were conducted in arable soil with relatively few litter resources; therefore, hemiedaphic Collembola may shift from litter-derived to root-derived resources. Similar to the results of Scheunemann et al. (2015), the hemiedaphic species *P. alba* incorporated more root-derived C than the euedaphic species *P. armata*.

The relatively low incorporation of root-derived resources into euedaphic species in rape and willow suggests that they more heavily rely on old C sources, i.e., soil organic matter and litter, than hemi- and epedaphic species in these cropping systems. Supporting this conclusion, Ponge (2000) found certain euedaphic species to preferentially consume humus rather than root tissue or fungal hyphae. Further, old soil C accounted for more than 50% of the body C of Collembola in maize fields even after prolonged growth of maize (Albers et al. 2006; Scheunemann et al. 2010). This is supported by the relatively high natural $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of euedaphic Collembola in rape and willow (Table S4), which correspond to the enriched $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of soil organic matter relative to plant material (Hyodo et al. 2010; Potapov et al. 2019). However, high $\delta^{15}\text{N}$ values in Collembola may also reflect trophic fractionation due to occupying higher trophic positions within the food web (Chahartaghi et al. 2005).

While the incorporation of root-derived C differed between functional groups in rape and willow, there was no significant difference between functional groups in grass (Fig. 4). This was mainly due to higher incorporation of root-derived C into

euedaphic species in grassland as compared to rape and willow. Roots of grass may be more palatable than those of rape and willow. This may especially be true for *P. armata*, since its natural abundance $\delta^{13}\text{C}$ values decreased from comparatively high values in rape and willow to low values in grass (Table S4), indicating a more direct trophic relationship to grass roots, presumably via feeding on roots, arbuscular mycorrhizal fungi, or root-feeding nematodes. Previous studies also found euedaphic Collembola species to shift their food preference from root C to soil organic C depending on resource availability (Gillet and Ponge 2003; Endlweber et al. 2009; Eerpina et al. 2017). In addition, high belowground C allocation in grass may promote its utilization by different functional groups of Collembola as well as their microbial prey.

Previous studies suggest that epedaphic species potentially have a high preference for aboveground resources such as microalgae, lichens, and organic matter deposited by plants, including pollen and honeydew from aphids (Scheunemann et al. 2010; Potapov et al. 2016a). However, the temporal variation in $\Delta^{13}\text{C}$ values of epedaphic and hemiedaphic species in individual cropping systems was synchronous with that of euedaphic species; since euedaphic species are unlikely to be linked to aboveground resources, the main source of their recently fixed C is likely to be root-derived. Although photoautotrophic microorganisms might be an important resource for Collembola in upper litter layers or extreme habitats such as rock surface (Potapov et al. 2018), their importance in presence of plant roots remains unknown. Further research separating different channels of recently fixed C to epedaphic Collembola is required.

Species-specific differences in the incorporation of root C

Functional group could only partially explain the variation in the incorporation of ^{13}C into Collembola species;

species within the same functional group also differed in the incorporation of ^{13}C supporting our third hypothesis. Notably, the variation was most pronounced in euedaphic species, with *P. armata* incorporating considerably more root-derived C than *S. denisi* (Fig. 5). In contrast to variations within epedaphic and hemiedaphic groups, this difference persisted in each of the studied cropping systems, indicating remarkable niche differentiation between euedaphic species.

Strong niche differentiation in euedaphic Collembola has also been observed by Potapov et al. (2016a), who found higher dependence on root-derived resources in *P. armata* than in *Isotomiella minor*, and by Fujii et al. (2016), who found incorporation of root-derived C into *Onychiurus flavescens*, but not into *I. minor*. While *Protaphorura* and *Onychiurus* belong to the family Onychiuridae, *Isotomiella* and *Stenaphorura* belong to families Isotomidae and Tullbergiidae, respectively, characterized by more slender bodies allowing to access smaller soil pores. Thus, the niche differentiation in euedaphic Collembola may be explained partly by morphological differences within functional groups (Potapov et al. 2016b).

More pronounced niche differentiation in euedaphic Collembola potentially points to higher demand for resource partitioning in the mineral soil. The relatively stable environment in mineral soil may facilitate resource exploitation and thereby competition, promoting the differential utilization of root-associated and litter/humus-associated resources among euedaphic species. By contrast, resources in surface soil presumably varied considerably between cropping systems and this likely contributed to the variable uptake of ^{13}C of species of the same functional group in epedaphic and hemiedaphic Collembola. For instance, ^{13}C enrichment in *L. paradoxus* was lower than that in the other epedaphic species in rape, but similar in grass and willow.

Collembola species with low incorporation of ^{13}C presumably rely less on root-derived C, but more on other unlabeled resources such as soil organic matter. Supporting this assumption, we found the incorporation of ^{13}C into Collembola species ($\Delta^{13}\text{C}$ values) to be negatively correlated with bulk tissue ^{13}C natural abundance of Collembola ($\delta^{13}\text{C}$ values) in rape and grass (Fig. 6). This is in line with previous studies indicating that low $\delta^{13}\text{C}$ values reflect preferential incorporation of recently fixed plant C; by contrast, high $\delta^{13}\text{C}$ values indicate high incorporation of C originating from soil organic matter and associated microorganisms (Potapov et al. 2016b, 2019). Interestingly, *L. paradoxus* in rape had low natural $\delta^{13}\text{C}$ values, but also low incorporation of ^{13}C , contrasting other epedaphic species (Fig. 5, Table S4). In addition, ^{13}C enrichment of *L. paradoxus* declined after it peaked at day 7. This suggests that, unlike the other epedaphic species, *L. paradoxus* incorporated recently fixed C from other photoautotrophs than plants, presumably algae or cyanobacteria.

Body size may be another factor affecting the incorporation of ^{13}C into Collembola species, since smaller species with higher mass-specific metabolic rates (Brown and Sibly 2006) may also have a higher rate of ^{13}C incorporation than larger species (Larsen et al. 2009). However, there was no significant correlation between body size and the incorporation of ^{13}C into Collembola species, suggesting that dietary differentiation may play a more important role in governing incorporation of root-derived C than body size. Although the present study cannot provide details on the exact mechanisms responsible for the differential incorporation of root-derived C into Collembola species, e.g., by feeding on different microorganisms, our results suggest that the differential use of basal resources may be an important mechanism favoring local coexistence of Collembola species.

Conclusions

Results of the present study demonstrate that the flux of root-derived C into soil microbivores, and thus to higher trophic levels of soil food webs, strongly varies between cropping systems. Cropping system not only affected the flux of root C into Collembola, with slower fluxes in rape than in grass and willow, but also the utilization of root-derived resources vs. litter/soil organic matter-derived resources by Collembola functional groups and species. Thereby, our findings suggest that the role of root-derived C as major resource fueling soil food webs varies markedly with cropping system, potentially due to differences in plant species/plant type and application of fertilizer. Future studies using novel techniques, such as compound-specific fatty acid, amino acid, and molecular gut content analysis, will allow deeper insight into the relative contributions of fungi and bacteria in channeling recently fixed C from roots into soil food webs of arable fields with different cropping systems and fertilizer regimes.

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Authors' contributions Stefan Scheu, Johanna Pausch, Nicole Scheunemann, and Lingling Shi designed the experiment. Zhipeng Li, Nicole Scheunemann, and Lingling Shi conducted the experiment. Zhipeng Li, Melanie M. Pollierer and Anton M. Potapov analyzed the data. Zhipeng Li wrote the manuscript, and Melanie M. Pollierer and Stefan Scheu revised it. All authors contributed critically to the drafts and gave final approval for publication.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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