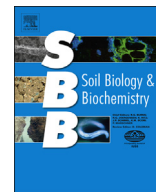




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Short communication

## Stable isotope composition of mycophagous collembolans versus mycotrophic plants: Do soil invertebrates feed on mycorrhizal fungi?



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## ABSTRACT

Ectomycorrhizal fungi constitute a large proportion of the belowground microbial biomass and contribute significantly to nutrient cycling, but their role in soil food webs remains poorly known. In this study, we compared the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of collembolans and mycoheterotrophic plants. Stable isotope composition of collembolans was very similar to those of mycotrophic plants associated with saprotrophic fungi. In contrast, mycotrophic plants associated with mycorrhizal fungi were enriched in  $^{15}\text{N}$  relative to collembolans by at least 5‰. Our data suggest that soil collembolans do not use mycorrhizal fungi as the main food source, and support an emerging view that extramatrical mycorrhizal mycelium can be retained in the soil to serve as a progenitor of stabilized soil organic matter.

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In forest ecosystems, 30–50% of the total primary plant production is allocated belowground as root litter and rhizodeposits (Litton et al., 2007). Having access to an ample C supply provided by dominant tree species, ectomycorrhizal (EM) fungi constitute a large proportion of the belowground microbial biomass in forest soils (Wallander et al., 2004, 2001; Mikusinska et al., 2013). This suggests that EM fungi can be an important food source for mycophagous soil animals. In turn, grazing by soil animals may affect the abundance of the extramatrical EM mycelium. As EM fungi compete with saprotrophic fungi for organic nitrogen compounds and other nutrients (Hättenschwiler et al., 2005), mycophagous animals can regulate C and N allocations among ecosystem pools by preferential feeding on mycorrhizal or saprotrophic mycelium (Boerner and Harris, 1991; McGonigle, 1995). Surprisingly, the participation of EM fungi in detrital food webs remains understudied.

A pronounced flux of carbon from living plant roots to animal decomposers has been recorded in field experiments which used whole-tree  $^{13}\text{C}$  labeling (Pollierer et al., 2007; Högberg et al., 2010). It was therefore suggested that collembolans and other soil animals feed actively on EM fungi (Pollierer et al., 2012). However, there is no conclusive evidence of the “root carbon” being assimilated by

soil animals via direct feeding on EM fungi. Both laboratory (Setälä, 2000) and field (Mikusinska et al., 2013) experiments demonstrated that the abundance of soil animals does not depend on the biomass of EM fungi. Moreover, only a few animal taxa (e.g. the oribatid mite *Opiella nova* and proturans) showed a clear negative response to a decreased flux of photosynthates from the canopy to the roots in a large-scale tree-girdling experiment (Remén et al., 2008; Malmström and Persson, 2011).

Elucidating the role of EM fungi in the soil food webs is of crucial importance for understanding the mechanisms controlling C cycling in EM-dominated ecosystems. This question can be addressed using a consistent difference in the isotopic composition of EM and saprotrophic soil fungi. Sporocarps of EM fungi are strongly enriched in  $^{15}\text{N}$  compared to sporocarps of saprotrophic fungi (Mayor et al., 2009). According to published data (e.g. Chahartaghi et al., 2005; Maraun et al., 2011), soil fungivorous animals (collembolans and oribatid mites) have relatively low  $\delta^{15}\text{N}$  values, suggesting a minor importance of EM fungi in their diet. Yet this notion remains ambiguous as there is only fragmentary information on the isotopic composition of extramatrical EM mycelium (Wallander et al., 2004; Mikusinska et al., 2013).

Trophic links of soil invertebrates can be clarified by comparing the isotopic composition of fungivores and reference groups of organisms gaining energy and nutrients either from EM or from saprotrophic fungi. Mycoheterotrophic (MH) plants lack chlorophyll and depend on their mycobiont for the supply of both C and N

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(Merckx, 2013). Most of MH plants share their EM mycobiont with autotrophic host plants (EM-MH plants), although some species depend on saprotrophic fungi (SAP-MH plants, Martos et al., 2009; Preiss and Gebauer, 2008). Therefore, the difference in isotopic composition between EM-MH and SAP-MH plants can be used for the identification of feeding on mycorrhizal or saprotrophic fungi. In this study, we aimed at assessing the role of EM fungi in the feeding of collembolans, one of the most abundant groups of fungal grazers in the soil. We expected that isotopic similarity of collembolans with EM-MH plants will confirm their feeding on EM fungi, whereas the similarity with SAP-MH plants will be evidence of trophic links with saprotrophic fungi.

To increase the number of observations, we compiled the published data on the isotopic composition of EM-MH and SAP-MH plants. This combined dataset was compared to our original data on the stable isotope composition of soil collembolans. The isotopic composition of soil animals, including collembolans, remains roughly similar across different forest habitats if normalized to the isotopic composition of dominant plant species (Chahartaghi et al., 2005; Klarner et al., 2013; Korobushkin et al., 2014). Similarly, the isotopic composition of MH plants may vary within and between ecosystems, but two main types (EM-MH and SAP-MH plants) remain distinct (Table 1).

Soil samples (including litter and upper 4–5 cm of mineral soil) and leaves of dominant tree species (*Picea abies* and *Betula pubescens*) were collected in three forest sites on podzoluvisol in the Moscow Region, Russia. Animals were extracted using Tullgren funnels in 80% alcohol and identified. Along with animals, a few samples of an EM-MH plant, *Monotropa hypopitys* were taken. Stable isotope analysis was conducted using a Thermo-Finnigan Delta V Plus continuous-flow IRMS; analytical details are given in Potapov et al. (2013). Data on the isotopic composition of EM-MH and SAP-MH plants were retrieved from nine published studies

(Table 1). To compensate for the variability of stable isotope baseline among different ecosystems, the isotopic composition was expressed as the enrichment factor ( $\epsilon$ ) relative to co-occurring dominant tree species ( $\epsilon = \delta_{\text{sample}} - \delta_{\text{reference}}$ ). In contrast to recent reviews, e.g. Zimmer et al. (2007), we used only upper canopy trees to avoid the influence of the “canopy effect” (Brooks et al., 1997) on the  $\delta^{13}\text{C}$  values of reference plants. One-way ANOVA with post-hoc Tukey unequal n HSD test (Statistica 8.0) was used to compare the mean  $\epsilon^{13}\text{C}$  and  $\epsilon^{15}\text{N}$  values. Standard Bayesian ellipses (R, SIAR package, Jackson et al., 2011) were used for estimating an overlap in the “isotopic niches” of plants and collembolans.

The EM-MH plants were strongly enriched in  $^{15}\text{N}$  ( $\epsilon^{15}\text{N} = 12.2\%$ ) compared with SAP-MH plants (2.6%,  $p < 0.001$ ) and collembolans (2.5%,  $p < 0.001$ ). The mean  $\epsilon^{13}\text{C}$  values failed to differ among groups, averaging about 6‰ (Table 1). There was a high overlap in the standard ellipse areas (56.4%) of collembolans and SAP-MH plants, but no overlap of these two groups and EM-MH plants (Fig. 1).

These data suggest a close similarity in the feeding mode of collembolans and SAP-MH plants. This assumption is only valid if the patterns of stable isotope trophic fractionation are similar in collembolans and MH plants. Both groups are heterotrophic and their isotopic composition depends primarily on isotopic composition of their food sources (Tiunov, 2007). EM-MH plants are on average enriched in  $^{15}\text{N}$  by 3.5‰ relative to sporocarps of their mycobionts (Trudell et al., 2003). A similar difference in  $\delta^{15}\text{N}$  values is usually observed between animals and their food (Post, 2002). In any case, possible differences in the patterns of trophic fractionation among trophic groups of MH plants and/or soil animals are unlikely to account for a pronounced difference in  $\delta^{15}\text{N}$  values between EM-MH plants and collembolans. Eventually, the lowest mean  $\epsilon^{15}\text{N}$  value in EM-MH plants was ca. 5‰ higher than the

**Table 1**  
Stable isotope composition ( $\epsilon^{13}\text{C}$  and  $\epsilon^{15}\text{N}$  values) of mycoheterotrophic plants (original and published data) and collembolans (original data). Enrichment ( $\epsilon$ ) was calculated as the difference in  $\delta$  values with dominating upper canopy plants. The mean values for trophic groups were calculated by averaging the mean values per species.

Species	Family	Source	n	$\epsilon^{13}\text{C}$ , ‰	$\epsilon^{15}\text{N}$ , ‰
<b>Mycoheterotrophic plants associated with ectomycorrhizal fungi (EM-MH plants)</b>					
<i>Monotropa hypopitys</i> L.	Ericaceae	Original data; Zimmer et al. (2007, 2008)	12	7.2 ± 2.0	13.1 ± 2.1
<i>Sarcodes sanguinea</i> Torrey	Ericaceae	Zimmer et al. (2007)	14	5.0 ± 1.4	15.0 ± 1.9
<i>Pteropora andromeda</i> Nuttall	Ericaceae	Zimmer et al. (2007)	9	3.0 ± 1.3	11.5 ± 1.4
<i>Corallorhiza maculata</i> Rafin	Orchidaceae	Zimmer et al. (2007)	10	7.0 ± 0.7	12.0 ± 2.0
<i>Neottia nidus-avis</i> L.	Orchidaceae	Zimmer et al. (2007, 2008); Gebauer and Meyer (2003), Bidartondo et al. (2004)	32	8.2 ± 1.0	11.3 ± 2.9
<i>Cephalanthera damasonium</i> albino Mill.	Orchidaceae	Julou et al. (2005)	10	9.0 ± 0.9	11.2 ± 1.5
<i>Cephalanthera longifolia</i> albino L.	Orchidaceae	Abadie et al. (2006)	9	4.3 ± 0.2	13.5 ± 1.6
<i>Epipactis helleborine</i> L.	Orchidaceae	Stöckel et al. (2014)	11	7.3 ± 0.7	10.5 ± 2.5
<b>Mean</b>			<b>8</b>	<b>6.4 ± 2.0</b>	<b>12.2 ± 1.5</b>
<b>Mycoheterotrophic plants associated with saprotrophic fungi (SAP-MH plants)</b>					
<i>Serapias parviflora</i> Parl.	Orchidaceae	Stöckel et al. (2014)	3	1.9 ± 0.3	2.0 ± 0.6
<i>Pseudorchis albida</i> L.	Orchidaceae	Stöckel et al. (2014)	6	4.9 ± 0.3	1.4 ± 1.3
<i>Gastrodia confusa</i> Honda & Tuyama	Orchidaceae	Ogura-Tsujita et al. (2009)	5	9.2 ± 1.3	2.8 ± 0.5
<i>Wulfschlaegelia aphylla</i> Sw.	Orchidaceae	Martos et al. (2009)	1	4.8	3.4
<i>Gastrodia similis</i> Bosser	Orchidaceae	Martos et al. (2009)	2	9.2 ± 3.3	3.3 ± 2.3
<b>Mean</b>			<b>5</b>	<b>6.0 ± 3.2</b>	<b>2.6 ± 0.8</b>
<b>Collembolans</b>					
<i>Ceratophysella</i> sp.	Hypogastruridae	Original data	2	7.7 ± 1.5	4.4 ± 0.3
<i>Folsomia quadrioculata</i> Tullberg	Isotomidae	Original data	5	5.2 ± 0.5	0.7 ± 0.9
<i>Parisotoma notabilis</i> Schäffer	Isotomidae	Original data	32	5.6 ± 0.9	1.1 ± 1.5
<i>Isotomiella minor</i> Schäffer	Isotomidae	Original data	6	5.7 ± 0.7	2.6 ± 1.9
<i>Lepidocyrtus lignorum</i> Fabricius	Entomobryidae	Original data	13	4.9 ± 0.6	2.9 ± 2.1
<i>Neanura muscorum</i> Templeton	Neanuridae	Original data	4	6.7 ± 1.0	4.0 ± 0.7
<i>Protaphorura armata</i> Tullberg	Onychiuridae	Original data	25	5.7 ± 1.0	4.5 ± 1.4
<i>Pogonognathellus</i> sp.	Tomoceridae	Original data	15	4.2 ± 0.8	0.9 ± 1.2
<i>Pseudachorutes</i> sp.	Neanuridae	Original data	10	6.7 ± 1.2	5.3 ± 1.6
<i>Pseudosinella alba</i> Packard	Entomobryidae	Original data	25	5.2 ± 1.1	2.3 ± 1.2
<i>Sminthuridae</i> g. sp.	Sminthuridae	Original data	9	4.4 ± 0.8	−1.4 ± 1.6
<b>Mean</b>			<b>11</b>	<b>5.6 ± 1.1</b>	<b>2.5 ± 2.0</b>

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