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Incorporation of carbon and nitrogen from leaf litter differing in structural compounds into soil microarthropods of a deciduous forest

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ABSTRACT

Detritivorous soil invertebrates process large quantities of leaf litter material. Focusing on decomposer (Oribatida) and predatory mites (Mesostigmata) we investigated the incorporation of resources from leaf litter rich (European beech, *Fagus sylvatica*) and poor (European ash, *Fraxinus excelsior*) in structural compounds using stable isotopes. Using litter mixtures we investigated if soil mites preferentially incorporate carbon (C) and nitrogen (N) derived from beech or ash leaf litter. Using the rotated-core method we established treatments with and without mycorrhiza as interactions between mycorrhiza and saprotrophic microorganisms may alter the availability of litter resources to soil invertebrates. Conform to our expectations primary decomposers incorporated more C and N than secondary decomposers or predators, but the contribution to body tissue element concentration was low suggesting that they predominantly rely on other resources than litter from the previous year. Generally, soil mites incorporated more C and N from ash than from beech litter, but this was less pronounced after 10 as compared to after 5 months, presumably due to fast decomposition of ash litter. In contrast to our expectations the use of litter resources by soil mites was little affected by mycorrhiza. Overall, the results underline that, at least during the first year of litter decay, leaf litter resources are of minor importance for soil mite nutrition, and this is particularly true for litter rich in structural compounds such as beech.

1. Introduction

Soil animal food webs are connected to the aboveground system via litter input and root derived resources with the root pathway being of significant importance (Ruf et al., 2006; Pollierer et al., 2012). In forests and scrublands typically about 70–90% of the net primary production is channeled as detritus into the decomposer system (Cebrian, 1999). Litter decomposition depends on various factors such as climatic conditions, litter quality and decomposer organisms (Swift et al., 1979; Couteaux et al., 1995).

Soil animals modify the decomposition of litter by translocation from the soil surface and mixing with mineral soil, fragmenting litter, and altering the activity and composition of microbial communities (Hanlon and Anderson, 1979; Hättenschwiler et al., 2005). Soil mites such as Oribatida and Mesostigmata are among the most widespread, abundant and species rich soil arthropods in forest soils (Schaefer, 1990), and play important roles in nutrient cycling (Berg et al., 2001). The diversity of soil mites is reflected by their diversity of feeding habits including primary and secondary decomposers as well as predators (Brussaard et al., 1997). Mesostigmata are mainly predacious (Koehler, 1999; Klarner et al., 2013), while Oribatida span over a wide range of trophic levels (Schneider et al., 2004).

Leaf litter is a challenging food source as nitrogen (N) concentrations are low compared to N demand of animals. Most litter carbon (C) is bound in structural compounds such as cellulose, hemicellulose and lignin, which are not readily available for animals (Hättenschwiler and Bretscher, 2001). The great majority of such structural litter compounds are processed by saprotrophic fungi and bacteria (Pomeroy, 1970; Petersen and Luxton, 1982). Therefore, litter C and nutrients are likely to be channeled to higher trophic levels, such as detritivorous animals and predators, via fungal and bacterial energy channels (Moore and Hunt, 1988; Moore et al., 1988; Pollierer et al., 2012). In European beech (*Fagus sylvatica*) forests the fungal energy channel benefits from beech roots releasing acids thereby favoring fungi (Rousk et al., 2009; Langenbruch et al., 2012). In addition, litter of beech is rich in structural compounds such as lignin which are degraded predominantly by fungi (De Boer et al., 2005). The bacterial energy channel is assumed to be more important in leaf litter material of high quality which is decomposing quickly and in

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processing easily available substrates such as sugars and amino acids (Moore et al., 2004; Wardle et al., 2004).

Besides saprotrophic microorganisms, mycorrhiza are also present in soils and they affect decomposition processes (Gadgil and Gadgil, 1971; Hodge et al., 2001), but the mechanisms are poorly understood (Koide and Wu, 2003). Mycorrhiza may dilute the flux of litter C into soil invertebrates due to the channeling of root C into soil food webs.

We investigated effects of leaf litter species differing in structural compounds on the transfer of litter C and N into soil mites (Cornwell et al., 2008; Vesterdal et al., 2008). In contrast to previous studies investigating either leaf litter C or N (Caner et al., 2004; Pollierer et al., 2007, 2009), incorporation of both C and N into soil mite species was investigated. To investigate the importance of structural compounds for the nutrition of soil mites and the transfer of C and N into the soil animal food web, European ash (*Fraxinus excelsior*) and beech litter differing markedly in structural compounds, but with similar N concentrations, were used. The impact of mycorrhizal fungi on decomposition and soil mite nutrition was investigated by rotating mesocosms at regular intervals thereby interrupting ingrowth of mycorrhizal hyphae (Johnson et al., 2001; Leifheit et al., 2014).

The following hypotheses were investigated: (1) primary decomposers incorporate most litter C and N via directly feeding on litter; secondary decomposers incorporate intermediate amounts as they also feed on bacteria and fungi processing older litter from previous years, rather than litter from the last growth period, whereas predators incorporate least amounts as they feed on prey also relying on root derived resources not labeled in this experiment; (2) soil mites incorporate more C and N from ash litter low in structural compounds and preferentially incorporate ash C and N in litter mixtures with beech; and (3) the presence of mycorrhiza dilutes litter C and N incorporation into soil microarthropods.

2. Material and methods

2.1. Study site

The experiment was set up in a beech forest in the Hainich National Park near Mülverstedt (51°06′N, 10°27′E) at 320 m asl. The Hainich National Park is located in Central Germany (Thuringia) and covers 16,000 ha. Mean annual temperature is 7.5 °C and mean annual precipitation is 670 mm (Meteomedia, station Weberstedt/Hainich, 51°10′N, 10°52′E). The beech forest stocks on Luvisol developed on loess underlain by Triassic Limestone. The forest floor is classified as mull-like moder with a mean thickness of the litter layer of 2.8 ± 0.1 cm (Jacob et al., 2010). The topsoil (0–10 cm) is rather acidic with a pH_{H2O} of 4.2–4.4 (Guckland et al., 2009).

2.2. Leaf litter

For ^{13}C labeling young beech and ash trees were exposed to $^{13}CO_2$ enriched atmosphere ($\delta^{13}C \approx 300‰$) in a greenhouse for 5 months; average temperature and humidity were 22.8 °C and 72%, respectively. For ^{15}N labeling and to establish similar nutrient conditions tree saplings were irrigated daily with a Hoagland-based nutrient solution containing 0.1 mM double labeled ammonium nitrate ($^{15}NO_3{}^{15}NH_4$, Euriso-top, Saint-Aubin, Essonne, France). Before experimental setup $\delta^{13}C$ and $\delta^{15}N$ values and chemical composition of labeled and unlabeled leaf litter material were determined. Lignin content was determined by Langenbruch et al. (2014) using the acetyl bromide method after Brinkmann et al. (2002). Cellulose was extracted with methanol:chloroform:water solution (2:2:1; modified after Dickson, 1979). The water–methanol fraction were kept for α-cellulose analysis according to Allen et al. (1974). $\delta^{13}C$ and $\delta^{15}N$ values of beech were 118.1 ± 1.7‰ and 3143 ± 229.2‰, respectively. $\delta^{13}C$ and $\delta^{15}N$ values of ash were 155.0 ± 5.2‰ and 26924 ± 1813‰, respectively. Labeled beech and ash litter had similar N concentrations (21.3 ± 0.4 and 19.9 ± 0.9 mg g^{-1} litter dry weight, respectively) and C-to-N ratios (23.1 and 22.9), but differed in concentrations of cellulose (135.2 ± 5.5 and 95.3 ± 4.2 mg g^{-1} litter dry weight) and lignin (see Langenbruch et al. (2014) (241.0 ± 4.1 and 178.1 ± 2.1 mg g^{-1} litter dry weight)).

2.3. Experimental setup

A total of 42 mesocosms were installed within a 50 × 50 m fenced area of the study site in December 2008. Undisturbed cores of the upper 5 cm of the mineral soil of a diameter of 24 cm were placed into plastic cylinders which were covered by 50 μm mesh at the bottom and by 1 mm mesh at the top allowing water to pass and hyphae to grow in, but preventing colonization by animals and ingrowth of roots.

The litter layer was removed and replaced by 14.4 g of labeled litter in pure treatments and mixed litter treatments receiving 7.2 g of each beech and ash litter; the amount of litter added resembled the amount present in the litter layer at the study site. Mesocosms were placed at a distance of 1 m from each other and 2 m apart from tree stems into the soil to a depth that the soil and litter layer inside matched those outside the mesocosms. Four treatments differing in litter composition were established: (1) labeled beech litter only, (2) labeled ash litter only, (3) mixture of labeled beech and unlabeled ash litter, (4) mixture of labeled ash and unlabeled beech litter. One half of the mesocosms were rotated each 14 days to interrupt hyphal connections between the outside and inner soil layers, thereby establishing treatments without (M−) and with mycorrhiza (M+). To investigate natural variations in stable isotope ratios in soil animals and to allow calculations of shifts in stable isotope values due to the addition of labeled litter, three control treatments with unlabeled litter were established: (1) pure beech litter, (2) pure ash litter, and (3) mixture of beech and ash litter. Unlabeled beech and ash litter was sampled in the Hainich National Park; signatures of $\delta^{13}C$ and $\delta^{15}N$ did not differ significantly and averaged −28.8 ± 0.5‰ and −0.9 ± 1.0‰, respectively (Langenbruch et al., 2014). Each treatment was replicated three times. Leaf litter derived $^{13}CO_2$ production was measured during the experiment (Langenbruch et al., 2014) and reached maximum levels after 5 months, i.e. by the time of the first sampling.

2.4. Stable isotope analyses of soil animals

Five (May 2009) and 10 months (October 2009) after establishment, the experiment was destructively sampled. For sampling of soil animals, the litter layer was separated from the mineral soil and animals in both layers were extracted by heat using a high-gradient canister method (Kempson et al., 1963). Thereafter, soil animals were transferred into 70% ethanol and identified to species level. For stable isotope analyses, two soil mite species (*Platynothrus peltifer*,*Steganacarus magnus*) from the sampling after 5 months and six soil mite species (*P. peltifer*, *S. magnus*, *Damaeus riparius*, *Nothrus silvestris*, *Uroseius cylindricus* and *Veigaia nemorensis*) from the sampling after 10 months were transferred into tin capsules at weights corresponding to a minimum of 10 μg N per sample. For most mite species several individuals had to be pooled and therefore only abundant species could be used. Analyses of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios were carried out using a coupled system consisting of an elemental analyzer (NA 1500, Carlo Erba, Milan, Italy) and a mass spectrometer (MAT 251, Finnigan, Bremen, Germany) (Reineking et al., 1993; Langel and Dyckmans, 2014). Abundances of ^{13}C and ^{15}N were expressed using