The oribatid mite *Scheloribates moestus* (Acari: Oribatida) alters litter chemistry and nutrient cycling during decomposition

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**A B S T R A C T**

It is widely accepted that microarthropods influence decomposition dynamics but we know relatively little about their effects on litter chemistry, extracellular enzyme activities, and other finer-scale decomposition processes. Further, few studies have investigated the role of individual microarthropod species in litter decomposition. The oribatid mite *Scheloribates moestus* Banks (Acari: Oribatida) is abundant in many U.S. ecosystems. We examined the potential effects of *S. moestus* on litter decomposition dynamics and chemical transformations, and whether these effects are influenced by variation in initial litter quality. We collected corn and oak litter from habitats with large populations of *S. moestus* and in microcosms with and without mites measured respiration rates, nitrogen availability, enzyme activities, and molecular-scale changes in litter chemistry. Mites stimulated extracellular enzyme activities, enhanced microbial respiration rates by 19% in corn litter and 17% in oak litter over 62 days, and increased water-extractable organic C and N. Mites decreased the relative abundance of polysaccharides in decomposing corn litter but had no effect on oak litter chemistry, suggesting that the effects of *S. moestus* on litter chemistry are constrained by initial litter quality. We also compared the chemistry of mite feces to unprocessed corn litter and found that feces had a higher relative abundance of polysaccharides and phenols and a lower relative abundance of lignin. Our study establishes that *S. moestus* substantially changes litter chemistry during decomposition, but specific effects vary with initial litter quality. These chemical transformations, coupled with other observed changes in decomposition rates and nutrient cycling, indicate that *S. moestus* could play a key role in soil C cycling dynamics.

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1. Introduction

The soil fauna consists of an array of species that collectively have a profound influence on ecosystem processes, including decomposition and nutrient cycling (Wolters, 2000; Coleman, 2008; Ekschmitt et al., 2008). Soil animals affect litter decomposition directly by ingesting and fragmenting litter and indirectly by altering the biomass and community structure of microbial decomposers (Hanlon and Anderson, 1979; Cortet et al., 2003; Coleman et al., 2004). However, faunal contributions to decomposition and nutrient cycling are variable and depend on the identity, density and activity of the resident species, as well as on their interactions with environmental conditions and substrate quality (Anderson et al., 1985; Bardgett and Chan, 1999; Lenoir et al., 2007; Ayres et al., 2010). Thus, predicting how changes in soil faunal communities will influence ecosystem function may require knowledge of individual species, their behavior, and their effect on soil processes under different environmental conditions.

One potentially important but largely unexplored way that soil animals could affect decomposition dynamics is by altering litter chemistry during decomposition. As plant litter passes through the animal digestive tract its chemical composition may be altered by enzymatic activity, organic matter mineralization and nutrient absorption (Gasdorf and Goodnight, 1963; Ziechman, 1994; Guggenberger et al., 1996; Hopkins et al., 1998; Gillon and David, 2001; Rawlins et al., 2006; Hedde et al., 2007; Filley et al., 2008; Geib et al., 2008). These changes in organic matter chemistry may have implications for soil aggregation and sorption dynamics, as well as for other biogeochemical processes that influence long-term C stabilization in soil (Golchin et al., 1994; Kleber et al., 2007). However, chemical transformations by soil animals have only been shown in a limited number of studies, have rarely used modern spectroscopic chemical approaches, and have focused mostly on macrofauna such as earthworms, millipedes and isopods (Teuben...
Oribatid mites are among the most abundant soil mesofauna, ranging from 25,000 to 500,000 individuals m⁻² in terrestrial ecosystems (Coleman et al., 2004). Studies have shown that the presence of oribatid mites can increase litter mass loss, stimulate microbial respiration rates and decrease fungal biomass (Siepel and Maaskamp, 1994; Kaneko, 1998; Hansen, 1999; Heneghan et al., 1999). However, little is known about their effects on other aspects of decomposition including the alteration of microbial extracellular enzymes and transformations of litter chemistry. Further, predicting the effects of oribatids on decomposition dynamics requires a better understanding of the ways in which individual species interact with litter quality (Hansen, 1999; Gergóc and Hufnagel, 2009).

Our recent experiments show that the oribatid mite Scheloribates moestus Banks (Scheloribatidae) is found in many Michigan ecosystems at densities approaching 200 individuals g⁻¹ dry litter (Wickings, Unpublished results). Both adults and juveniles may contribute significantly to decomposition through feeding on litter and microbes as well as through the production of feces. Given its population size and potential activity, S. moestus may play a key role in regulating decomposition in cultivated and native ecosystems. Our overall objective was to evaluate the potential effects of S. moestus on corn and oak litter decomposition dynamics and, more specifically, to determine whether S. moestus changes C and N cycling rates, enzyme activities, and chemical transformations in decomposing litter.

2. Methods

2.1. Litter and mite collection

Red oak (Quercus rubra L.) and corn (Zea mays L.) leaf litter were collected from the Michigan State University W.K. Kellogg Biological Station Long-Term Ecological Research Site (KBS, LTER) in October 2008. Micro-invertebrates were extracted from litter using Berlese funnels (Bioquip, Rancho Dominguez, CA) over a 3 d period into litter-sized plastic boxes lined with a moistened plaster-charcoal mixture (10:1 by weight). S. moestus was identified from samples and compared with type specimens from the Museum of Comparative Zoology, Harvard University, Cambridge, MA. Approximately 4000 S. moestus adults were collected in total (approximately 3000 individuals from corn, 1000 individuals from oak) and all individuals were transferred to separate live boxes to avoid predation by other arthropods. Approximately 2 g of either corn or oak leaf litter, moistened with deionized water, were placed in each box to provide food and habitat for S. moestus. After micro-invertebrates were extracted, corn and oak litter were removed from Berlese funnels and dried completely at 60 °C. All litter was cut and sieved to fragments ranging 2–5 mm after drying and further defaunated using two successive freeze–heat cycles (−80 °C and +80 °C) similar to those used by Bardgett et al. (1998).

2.2. Microcosm setup

Microcosms consisted of a 70 mL polypropylene bottle (litter arena), from which the bottom was removed and replaced with 38 μm stainless steel mesh, contained within a 120 mL glass jar. Before being placed in jars, 120 litter arenas received 1 g of defaunated corn or oak litter (n = 60 corn and 60 oak arenas). Once litter was arranged in an arena, it was soaked in a litter homogenate for 2 h to inoculate the microcosms with microbes. Homogenates were created by agitating 500 g of field-moist corn or oak litter in 4 L of deionized water for approximately 15 m. Suspensions were then filtered through a paper filter (Whatman, grade 1, particle retention 11 μm) to remove most particulate organic matter while retaining bacteria or fungal spores. After soaking, arenas were allowed to drain for 5 h before incubating in the dark at 22 °C for 5 d to allow microbial activity to increase. At the end of the 5-d incubation period, all arenas were placed into glass jars. In an effort to maintain adequate litter moisture contents, we placed 10 mL of water in the bottom of each jar. The litter arenas were elevated ~5 mm above the water using polypropylene stands. Twenty adult individuals of S. moestus were added to each of 60 arenas (n = 30 corn and 30 oak) with the remaining 60 arenas receiving no mites. Mite numbers were chosen to be consistent with densities of S. moestus measured in field sites at KBS (Wickings et al., Unpublished results). All microcosms were covered with plastic wrap to retain moisture but still allow for some gas exchange. Microcosms were kept at approximately 21 °C on a 12 h light–dark cycle for the duration of the experiment (62 d).

2.3. Microcosm analysis

At 6, 13, 22, 34, 48 and 62 d of incubation, 20 microcosms were destructively harvested for the measurement of enzyme activity, inorganic N, and dissolved organic carbon (DOC) and nitrogen (DON). Numbers of live mites were recorded at each harvest date at 400× magnification.

2.3.1. Litter C min and composition

At 3-d intervals, the plastic covering was removed from 20 litter arenas, which were then transferred to dry 120 mL jars and capped with lids fitted with rubber septa to quantify microbial respiration rate. The arenas used for CO₂ measurements were randomly selected at the beginning of the experiment. These same arenas were used for all CO₂ measurements and were subsequently the last to be destructively harvested. CO₂ concentration of the jar headspace was measured using an LI-820 infrared CO₂ analyzer (LICOR Biosciences, Lincoln, NE) at 30-m intervals over the course of 1 h (0, 30 and 60 m) and used to determine production rate (mg CO₂–C g⁻¹ litter d⁻¹).

Chemical composition of litter from time zero and after 62 d of decomposition was determined using pyrolysis gas chromatography–mass spectroscopy (py-gc/ms) using previously described methods (Grandy et al., 2009; Wickings et al., 2010). Briefly, samples were pulse-pyrolyzed in quartz tubes on a Pyroprobe 5150 (CDS Analytical Inc., Oxford, PA) using a pyrolysis temperature of 600 °C. Pyrolysis products were transferred onto a gas chromatograph (Trace GC Ultra, Thermo Scientific, West Palm Beach, FL) where they were further separated upon passage through a heated, fused silica capillary column (60 m × 0.25 mm i.d.). GC oven temperature was increased from 40 to 270 °C at a rate of 5 °C min⁻¹ with a final temperature ramp to 310 °C at 30 °C min⁻¹. Finally, compounds were transferred to a mass spectrometer (Polaris Q, Thermo Scientific, West Palm Beach, FL) via a 270 °C heated transfer line. The abundance of all ions was scaled relative to the largest peak, Peaks were compared to reference spectra using the Automated Mass Spectral Deconvolution and Identification program (AMDIS V 2.65) and the National Institute of Standards and Technology library (NIST).

In order to better understand the direct effects of S. moestus on litter chemistry we also analyzed the chemical composition of its feces. Two additional S. moestus live boxes, containing approximately 1000 adult mites each, were also maintained for the duration of the study. Four nylon filter disks were placed in each live box and each disk received approximately 1 g of litter (one box contained corn and one contained oak). Live boxes were kept at approximately 21 °C and deionized water was added to the plaster base of each box as needed to maintain adequate moisture.
2–3 d intervals, mite feces were collected from the surface of each filter disk using a modified vacuum apparatus consisting of a 70 μL quartz tube filled half way with glass wool and attached to a vacuum pump. All feces were stored at −80 °C prior to analysis. Oven-dried (60 °C) and pulverized samples of mite feces were analyzed using py-gc/ms following the procedures outlined above. Analyzing fecal material chemistry allowed us to compare chemistries among the following: 1) initial undecomposed litter; 2) litter plus microbes after decomposition for 62 d; 3) litter plus microbes plus mites after 62 d of decomposition (mites were removed from litter prior to chemical analysis); and 4) mite feces after feeding on litter. Juvenile S. moestus were present in live boxes after approximately one month and we were unable to separate their feces from that of the adults although their numbers were low relative to adults. We attempted to collect mite feces from oak for three months but were unable to obtain enough material for analysis.

2.3.2. Extracellular enzyme activity

The activity of seven extracellular enzymes was analyzed using procedures outlined in Saija-Cork et al. (2002) and Grandy et al. (2007). Briefly, the activities of N-acetyl- β-D-glucosaminidase (chitinase), β-glucosidase (cellulase), β-1,4-celllobiosidase (cellulase), tyrosine amino peptidase and acid phosphatase were assessed in black, 96-well microplates using substrates containing fluorescent molecules methylumbelliferone (MUB) and methylcoumarin (MC). The activity of urease was measured using colorimetric methods outlined in Sinsabaugh et al. (2000) and modified for analysis in 96-well microplates. Finally, the activity of the oxidative enzyme phenol oxidase was measured in clear 96-well microplates using L-3,4-dihydroxyphenylalanine (l-DOPA). Litter suspensions were prepared using 0.25 g subsamples of litter and deionized water for 1 h on a bench-top shaker (200 rpm). Mite slurries were then passed through a Whatman GF/A filter and filtrates were stored at −20 °C until further analysis. Bioavailable nitrate and ammonium were quantified in litter filtrates using photo- metric experiments (Sinsabaugh et al., 2000; Doane and Horwath, 2003). Total organic C and N were also measured on filtrates using a Shimadzu TOC-TN combustion analyzer (Shimadzu Scientific Instruments, Columbia, MD) and leaf litter C and N values were determined using an elemental analyzer (Costech ECS 4010, Costech Analytical Technologies, Inc., Valencia, CA). Total organic N was determined by subtracting nitrate and ammonium from total N.

2.4. Statistical analysis

Microbial respiration data were analyzed using mixed model analysis for repeated measures in SAS (PROC MIXED) with mite presence/absence and time as fixed effects and block as a random effect. Extracellular enzymes were analyzed using two-way analysis of variance in SAS (ANOVA) with mite presence/absence and time as treatment factors. Nitrate, ammonium, total organic nitrogen, total organic carbon and molecular chemical data were all analyzed using one-way analysis of variance in SAS (ANOVA). Litter types were analyzed independently for both one- and two-way analyses.

3. Results

3.1. Mite numbers and observations of feeding activity

The number of mites per microcosm dropped from 20 to a mean of 15 in corn and 13 in oak within one week of the start of the experiment. This number was maintained throughout the experiment in corn microcosms, however, the number of live mites in oak litter dropped to a mean of 4.5 individuals g⁻¹ of litter from 48 to 62 d of incubation. Juvenile mites were observed in both corn and oak microcosms beginning on day 34 and were present in low numbers for the remainder of the incubation. Daily observations confirmed that both adults and juveniles fed throughout the experiment and the majority of individuals examined contained multiple fecal boluses. Additionally, slide mounts of fecal material during the course of the experiment showed that boluses contained both plant and microbial material.

3.2. Litter C and N dynamics

Corn and oak litter differed qualitatively at the start of the experiment. Although corn litter had a higher proportion of lignin than oak (38 vs. 14% of sample composition) it also had higher proportions of nitrogen bearing compounds (13 vs. 5%) and polysaccharides (20 vs. 9%). Additionally, oak litter had a higher proportion of lipids (50 vs. 11%) and a higher C/N ratio than corn. CO₂ flux was higher in corn than in oak microcosms for the duration of the incubation (Fig. 1). Mites increased cumulative CO₂ production by 19% in corn (F₁, 168 = 23.00, P < 0.0001) and 17% in oak (F₁, 168 = 51.72, P < 0.0001). The C/N ratio of oak increased through time regardless of whether or not S. moestus was present. In contrast, corn C/N ratios only increased during decomposition in the absence of mites (Table 1).

Polysaccharide relative abundance increased in corn over 62 d of decomposition in the absence of mites (F₂, 6 = 11.01, P < 0.01) (Fig. 2 top). This increase was due primarily to the compound 2,3-dihydrobenzofuran and was not observed when mites were present (Appendix Table 1). Oak litter was dominated by lipids which comprised 40–50% of all identified compounds. Of the lipids, present, 60–90% were long-chain (>C20) compounds. Unlike corn, the chemistry of oak litter was not affected by the presence of mites (Fig. 2 bottom).

3.3. Fecal material chemistry

Mites that were fed corn litter generated feces that were chemically different from the original litter (Fig. 2 top). While the relative abundance of lignin was lower in feces than litter, that of phenol was higher (Fig. 2 top). In addition, polysaccharide relative abundance was significantly higher in feces than in both the initial litter and in litter decomposed for 62 d with microbes and mites. Ratios of lignin to nitrogen, and lignin to polysaccharides were also lower in feces than in corn litter by approximately 88 and 87% respectively. Further, the relative abundance of five compounds including one polysaccharide, a phenol, a compound of unknown origin and two lignin derivatives differed between feces and litter (Appendix Table 2). We planned to also include feces from oak-fed mites in our analyses but were unable to gather an amount sufficient for analysis.

3.4. Enzymes – extracellular enzymes within litter

The presence of mites altered the activity of both hydrolytic and oxidative extracellular enzymes. In corn microcosms, the activities of urease (32 d, $F_{5, 48} = 2.88$, $P < 0.05$), glucosidase (48 d, $F_{5, 48} = 2.49$, $P < 0.05$) and acid phosphatase (48 d, $F_{5, 40} = 7.32$, $P < 0.05$) were greater in the presence than absence of mites (Fig. 3). The presence of mites also resulted in a 30% increase in the activity of phenol oxidase averaged across sample dates ($F_{1, 48} = 8.20$, $P < 0.01$) (Fig. 3). The most marked increase occurred in week 3, when oxidative activity was approximately 2.5 times higher in microcosms with than without mites. Chitinase, cellobiosidase and tyrosine amino peptidase activities in corn were not affected by mites in oak litter. In oak litter, the presence of mites stimulated glucosidase ($F_{5, 48} = 3.48$, $P < 0.01$) and chitinase ($F_{5, 48} = 3.64$, $P < 0.01$) activity at 48 and 62 d but suppressed chitinase, glucosidase and phosphatase activity during the initial week of the experiment (Fig. 4). Phenol oxidase activity was also marginally suppressed by the presence of mites during sampling week 1 but was greater in microcosms with than without mites during the following week ($F_{5, 48} = 2.50$, $P < 0.05$). Urease, cellobiosidase and tyrosine amino peptidase activities were not affected by mites in oak litter.

3.5. Enzymes – enzymatic potential of S. moestus

Chitinase was the most active enzyme detected within S. moestus averaging 62.7 μmol h$^{-1}$ g$^{-1}$ dry mite biomass followed by cellulase, phosphatase and peptidase (44.8, 17 and 0.13 μmol h$^{-1}$ g$^{-1}$ dry mite biomass, respectively). Urease and phenol oxidase activities were not detected in S. moestus.

3.6. Aqueous C and N in microcosms

The presence of mites led to a significant increase in available nitrate, ammonium and both dissolved organic C and N (Tables 2 and 3). The effects of mites on ammonium concentrations peaked in corn litter at 34 d (4.9 fold increase) and in oak litter at 13 d (12.26 fold increase). In contrast, ammonium concentrations were greatest in corn microcosms without mites at 13 d. Mites increased nitrate concentrations in corn litter at 34 d (35.19 times more than in litter without mites), as well as dissolved organic C and N (1.3 and 4.2 times more, respectively) (Table 3).

4. Discussion

The soil fauna strongly influences ecosystem processes but the effects of individual species on C and N cycling and microbial activity during decomposition remain contentious (Ayres et al., 2010). Further, the effects of soil animals on changes in litter chemistry, extracellular enzyme activities and other key ecosystem processes during decomposition are poorly understood but could have a substantial, long-term effect on soil C cycling dynamics. We found that the widely distributed and often abundant oribatid mite S. moestus: 1) increased the mineralization of C and N; 2) accelerated extracellular enzyme activities; 3) altered the molecular chemistry of decomposing litter; and 4) interacted with variation in initial litter chemistry, indicating that the overall effect of S. moestus on ecosystem processes depends upon substrate quality.

4.1. C and N cycling and enzyme activities

Some microarthropods have been shown to stimulate C mineralization (Kaneda and Kaneko, 2008) but studies focusing on oribatids are rare (c.f. Kaneko 1998). We observed that C mineralization in the presence of S. moestus increased by 19% in corn and 17% in oak litter. Previous estimates suggest that the entire mesofaunal community directly accounts for approximately 5% of the CO2 released from soil during decomposition and mathematical models predict that oribatids should have little impact on microbial C mineralization (Berg et al., 2001). Although our microcosms do not simulate field conditions with fluctuating environmental conditions and substrate availability, our results indicate that some species of oribatid mites can strongly enhance mineralization rates (Siepel and Maaskamp, 1994). We also show that S. moestus increases concentrations of both nitrate and ammonium in decomposing litter. The increases in inorganic N that we observed were temporally variable but generally similar to or greater than those found in studies using collembolans or other soil animals (Ineson et al., 1982; Anderson et al., 1985; Bardgett and Chan, 1999). The observed changes in C and N cycling are likely due to the direct effects of S. moestus on organic matter mineralization as well as to enhanced microbial enzyme activities and decomposition rates.
when animals are present (Petersen and Luxton, 1982; Kandeler et al., 1999; Ayres et al., 2010).

Indeed, we found that extracellular enzyme activity was generally higher in litter with mites than without, ranging from 1.3...
to 2.4 times higher in corn litter and 1.2 to 5 times higher in oak litter. The increases in extracellular enzyme activity may have resulted from litter fragmentation, which can increase microbial access to previously protected plant polysaccharides (Moorhead and Sinsabaugh, 2006; Saqib and Whitney, 2006; Herman et al., 2008). Microbial activity and extracellular enzyme activities may have also been stimulated by microbial grazing as well as the addition of labile mite feces with relatively low ratios of lignin:nitrogen and lignin:polysaccharide (Jenkinson et al., 1985; Schimel and Goodnight, 1963; Ziechman, 1994). Since we found no evidence for oxidative enzyme activity in the mite gut, the low percentage of lignin in feces likely resulted from selective feeding on labile microbial and plant compounds (Hubert et al., 2000).

While selective feeding likely explains differences in lignin relative abundance between fecal material and unprocessed plant litter, differences in other chemical constituents may have been due to enzymatic activity within the *S. moestus* gut. We found that *S. moestus* had high activities of chitinase (27 times higher than plant litter), cellulase (8 times higher) and phosphatase (5 times higher), indicating that along with other microarthropods it possesses a variety of digestive enzymes capable of catabolizing diverse organic compounds (Siepel and de Ruiter-Dijkman, 1993; Berg et al., 2004; Norton and Behan-Pelletier, 2009). Our study did not determine the origin of this enzymatic activity but microbial gut symbionts within the oribatid gut likely play a key role in gut enzyme production and litter processing (Stefaniak and Seniczak, 1976; Seniczak and Stefaniak, 1978; Ayres et al., 2010). Whether these enzymes are produced by the animal itself or by gut-inhabiting microbes, the soil animal gut is thus a hotspot of enzymatic activity, as well as of chemical transformations.

### 4.3. Litter quality

Changes in litter chemistry due to the presence of *S. moestus* were limited to corn litter. We attribute this to the initial differences in chemical structure of corn and oak litter and its effects on microbial activity. Before decomposition, oak litter had a greater relative abundance of long-chain lipids, which are found in undecomposed plant material (Saccini et al., 2009) and likely originated in the thick, waxy cuticle of oak leaves. While lignin may break down relatively rapidly (Rasse et al., 2006; Denef et al., 2009), long-chain lipids can be very recalcitrant and selectively preserved during decomposition (Lorenz et al., 2007; Grandy et al., 2008; Denef et al., 2009). Indeed, C and N mineralization rates and transformations within the mite gut, although we cannot rule out the possibility that the continuing activity of microbes and extra-cellular enzymes in feces during the time between defecation and sample collection also played a role. Our results contrast with two past reports using different oribatid species, which showed higher lignin concentrations in feces than in unprocessed litter (Gasdorf and Goodnight, 1963; Ziechman, 1994).

### 4.2. Litter chemistry

Determining the effects of soil animals on C and N cycling also requires a more complete understanding of how they influence litter chemistry during decomposition, as variations in chemistry can affect nutrient cycling and long-term soil organic matter dynamics (Rubino et al., 2009; Kleber and Johnson, 2010). Recent studies have shown that ecosystem N enrichment (Neff et al., 2002; Gallo et al., 2005; Grandy et al., 2008) and agricultural conversion (Grandy et al., 2009; Wickings et al., 2010) can alter organic matter dynamics (Rubino et al., 2009; Kleber and Johnson, 2010). Recent studies have shown that ecosystem N enrichment (Neff et al., 2002; Gallo et al., 2005; Grandy et al., 2008) and agricultural conversion (Grandy et al., 2009; Wickings et al., 2010) can alter organic matter chemistry. Wickings et al. (2010) argued that differences in litter chemistry during decomposition may arise from variations in decomposer communities. However, these studies were not able to isolate the effects of decomposer communities from other abiotic or biogeochemical processes that influence soil C dynamics in the field. Our study firmly establishes that a single oribatid species can influence changes in litter chemistry during decomposition.

We compared the chemistry of decomposing litter with and without mites and found that *S. moestus* decreased the relative abundance of polysaccharides in corn litter by 7% during decomposition. This difference is likely due in part to the indirect effects of *S. moestus* on microbial activity. *S. moestus* stimulated microbial extracellular enzyme activity in litter, and changes in enzyme activity may alter the trajectory of chemical changes in decomposing organic matter (Grandy et al., 2008, 2009; Wickings et al., 2010).

We also found that *S. moestus* feces, which contain both plant and microbial material, are relatively depleted in lignin, enriched in phenols and possess lower ratios of lignin:polysaccharide and lignin:nitrogen than unprocessed plant litter. These measured differences between litter and feces chemistry primarily reflect

### Table 2

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<th>NH$_4$$^+$-N (µg g$^{-1}$ dry litter)</th>
<th>NO$_3$-N (µg g$^{-1}$ dry litter)</th>
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<tr>
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### Table 3

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<th>DON (mg g$^{-1}$ dry litter)</th>
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<tr>
<td></td>
<td>Corn 13</td>
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enzyme activities, all indicators of microbial activity, were lower in oak litter. This provides additional evidence that oak litter was more recalcitrant than corn litter, but also points to the probability that the effects of decomposer communities on litter chemical transformations may depend upon the quality of the substrate being decomposed (Kampichler and Bruckner, 2009; Wickings et al., 2010).

4.4. Summary

Soil animals are broadly known to have a range of effects on decomposition dynamics. However, at a finer-scale there remain many key uncertainties, including the effects of individual species on decomposition processes, and the degree to which animals can alter the chemistry of litter during decomposition (Ayres et al., 2010). We have demonstrated that the presence of a single orbicatid mite species can enhance C mineralization rates by almost 20%, stimulate hydrolytic and oxidative enzyme activities and change litter chemistry during decomposition. No other studies have come to our attention that show molecular-scale differences in the chemistry of orbicatid feces compared to litter, or of litter decomposing with and without mites. These changes in litter chemistry during decomposition varied with initial substrate quality and could have long-term implications for soil C cycling. Future studies comparing different orbicatid mite species, different groups of microarthropods and different trophic levels under more realistic conditions will help elucidate the effects of individual species and functional groups on decomposition.

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Appendix. Supplementary data

Supplementary data related to this article can be found online at doi:10.1016/j.soilbio.2010.10.023.

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Appendix. Supplementary data

Supplementary data related to this article can be found online at doi:10.1016/j.soilbio.2010.10.023.

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