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Original article

Mechanical fragmentation enhances the contribution of Collembola to leaf litter decomposition

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ABSTRACT

Soil fauna influence the decomposition and nutrient mineralization of leaf litter; however, the specific contributions of mechanical fragmentation (macrofauna activity) and meso-fauna to nutrient mineralization, and their interactions with litter quality, require further study. Our aim was to investigate the independent and interactive effects of litter quality, mechanical fragmentation, and Collembola density on the litter decomposition process. Intact and fragmented leaf litter from two tree species with contrasting leaf litter quality were incubated in laboratory microcosms with high and low Collembola densities. Mass loss, C, and N concentrations of the leaf litter were measured. The results showed that fragmented, low C:N ratio litter with high Collembola density had the fastest rates of decomposition and C, N mineralization, while the lowest decay rates were measured in high C:N ratio litter with low Collembola density, regardless of fragmentation. Mechanical fragmentation alone could not significantly enhance the litter decomposition in either litter type without the presence of Collembola. Meanwhile, high Collembola density without mechanical fragmentation did not significantly achieve faster litter decomposition. However, mechanical fragmentation had a positive effect on increasing N concentrations and supplied with litter of higher C:N ratio. Presence of Collembola enhanced mass loss and C, N mineralization in decomposing litter of either type significantly associated with fragmentation. The positive interaction between mechanical fragmentation and Collembola reported here emphasizes the importance of multiple trophic interactions for regulating decomposition processes, including that of physical and biological interactions among all functional groups.

1. Introduction

Leaf litter quality and soil fauna are acknowledged as important factors that control the decomposition dynamics of substrates [30,39,61], particularly in humid tropical forests [26,27,32,49,67]. Different functional groups of soil fauna contribute differently to litter decomposition [8]. The most basic functional distinctions among soil fauna groups are fragmenters (i.e., shredders and comminutors), grazers (i.e., microbivores), and predators [16,22,41]. Fragmenters are primarily macrofauna, such as earthworms, millipedes, termites, and isopods, which alter resource availability by modifying the physical properties of litter [5,17,54]. The fragmentation of plant litter through biting and "external rumen digestion" by soil fragmenters augments food resources for soil microfauna and mesofauna [7]. In addition, fragmentation increases the surface area of the litter substrate, allowing microbes to access nutritious internal tissues, which in turn influences leaf litter decomposition [12,16,22]. Some studies have shown that macrofauna play an important role in decomposition, through both fragmentation and digestion [33,35,40,48,55], but few studies have discussed the contributions of mechanical fragmentation by soil fragmenters during the decomposition process.

Collembola are often among the best-represented soil mesofauna groups, in terms of species richness and abundance, and have been shown to affect leaf litter decomposition and nutrient mineralization by stimulating the activity of microorganisms and by increasing both nutrient mobility and stability in terrestrial ecosystems [1,18,23,37,38,43,50]. However, several studies have produced conflicting results, whereby different abundances or richness of Collembola have been shown to enhance [31,36], or not affect [9,13] the mass loss of decomposing litter. In comparison, substrate quality is known to be important in determining the effects of Collembolan activity [52].

Furthermore, there is an interaction between plant litter quality and soil fauna that potentially influences decay rate within the same habitat [68,69]. Numerous studies have indicated that the

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interaction between litter quality and soil fauna (including Collembola) may positively affect the decomposition of both high and low quality litter, as well as plant growth in forest ecosystems [6,51,56,58,63,68,70]. In contrast, several studies have also demonstrated that interactive effects do not exist between litter quality and soil fauna during litter decomposition processes [13,26,49]. The difference between these results might reflect the fact that there are multiple mechanisms by which fauna can affect function, which might be, in turn, dependent on specific taxa, environmental factors and time [53,58]. So this contradictory evidence shows that the mechanism that multiple trophic groups of soil fauna interact with litter quality requires further research. The direct and indirect effects of soil functional groups on decomposition are difficult to quantify in natural ecosystems, because the activities of the organisms occur simultaneously, often at different spatial and temporal scales, and are tightly intertwined with vegetation changes (i.e., litter quality) across environmental gradients [10,20,23,44,51,60]. Hence, microcosms provide opportunities for exploring different factors that may affect litter decomposition both separately and collectively, and have been shown to provide powerful insights into the litter decomposition process.

The aim of this study was to determine the individual influences and interactions of litter quality, mechanical fragmentation, and Collembola abundance on litter decomposition and mineralization. We incubated soil microcosms in a laboratory experiment designed to address the following questions: 1) does Collembola abundance affect decomposition rate, C and N mineralization; 2) are the influences of Collembola on decomposition affected by litter quality; 3) does mechanical fragmentation alter the relationship among Collembola, litter quality, and microbial biomass, and hence the decomposition rate? Mechanical fragmentation allowed us to decouple the physical effects of increased litter surface area from the biological effects associated with soil macrofauna, such as increased substrate inoculation with bacterial cells and fungal spores. We hypothesized that mechanically fragmented litter would increase mass loss by providing an increased surface area and substrate accessibility for microorganisms; consequently, increased Collembola abundance was expected to positively affect decomposition by influencing litter quality (i.e., C, N). Furthermore, we hypothesized that the influence of Collembola on decomposition would decrease with higher quality substrates (low C:N ratio) compared with lower quality substrates (high C:N ratio) based on initial low N availability and high C:N ratio, which limit microbial activity instead of Collembola abundance, and would increase when the litter was mechanically fragmented.

2. Materials and methods

2.1. Overview of the experimental design

Soil microcosms were constructed to study the independent and interactive effects of litter quality, litter fragmentation, and Collembola abundance on the decomposition of organic matter. Litter quality was manipulated by using leaf litter from two dominant tree species from a tropical seasonal rain forest located in the Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences (650–750 m in elevation, 101° 11′ E, 21° 56′ N; see details in Ref. [70]). Two species of foliar litter, of varying substrate quality, were selected for the study. *Lasiococca comberi* var. *pseudoverticellata* (Euphorbiaceae) (N = 16.7%; C:N = 26.32 ± 0.52) leaves have a higher concentration of N and lower C:N than *Pometia tomentosa* (Sapindaceae) (N = 11%; C:N = 46.69 ± 3.19). Therefore, *L. comberi* var. *pseudoverticellata* was used to represent a relatively high-quality litter and *P. tomentosa* as a relatively low quality litter [61]. Leaves from the two tree species were used in two different treatments: (1) intact litter where leaves were not altered and (2) mechanically fragmented leaves using scissors to cut leaf materials into pieces of ~2 mm wide and ~4–5 cm long. Each microcosm contained intact or fragmented litter from one tree species, and was randomly assigned to two decomposer treatments: (1) microorganisms only (M), and (2) microorganisms + Collembola (M + C). Microorganisms included fungi, bacteria. And nematodes, rotifers, protozoans, and tardigrades are categorized as microfauna. The soil and Collembola used for microcosm construction were extracted from four 1 m^2 plots at the forest site of XTBG. The soil was a red Ultisol (i.e., red clay soil), which had a soil organic matter content of 39.03 g kg^{-1}, total N of 2.29 g kg^{-1}, and C:N ratio of 17.04. Random subsets of 6 replicates for each treatment were destructively sampled after 0, 50, 150, and 300 d of incubation, and were analyzed for mass loss and litter decay rates. Chemical analyses of decomposing litter were performed from collected samples at 0, 150, and 300 d. In brief, the experiment was carried out using a factorial design which included 2 litter treatments (high and low) × 2 fragmentation treatments (intact and fragmented) × 2 soil mesofauna treatments (present or absent) × 6 replicates × 4 collection days, producing a total of 192 microcosms.

2.2. Soil and pre-treatments

Soil samples were collected in October 2005 from the mineral layer (0–20 cm) of four 1 × 1 m^2 plots in the seasonal tropical rain forest. After sampling, soils were sieved through 5 mm mesh to remove rocks, roots, and macro invertebrates. Fauna were removed from the sieved soils by freezing at −20 °C for 3 d [42]. After thawing for 2 d, the soils were refrozen under the same conditions. The freeze–thaw cycle was conducted 3 times to ensure efficacy. To build the microcosms, we added 500 g of mixed pretreated soils to cylindrical plastic pots of 14 cm in diameter and 15 cm in height. Drainage holes in the bottom of the pots were covered with 1 mm mesh before the soil was added. The soil moisture was maintained at 30% by-weight for the duration of the experiment.

2.3. Microcosm construction

Microcosms containing defaunated soil were inoculated with microorganisms and Collembola, according to the appropriate experimental treatment. To ensure that the "background" microorganisms were similar in all containers, we thoroughly ground and mixed 2.5 kg of fresh litter and surface mineral soil with 5 L of sterilized tap water for 2 min. We then added 10 ml of the resulting litter, and the soil suspension was added to each experimental container (microcosm) after coarse particles had settled.

Soil fauna were obtained from four 1 m^2 forest floor litter samples collected from subplots in the field, and placed in Tullgren funnels for 3 d. Soil arthropods were extracted in jars from litter and Collembola were collected from jars with a brush pen, then placed in a separate large pot (30 cm diameter, 30 cm height) containing defaunated soil every half day, and were cultivated for 2 weeks. Soil in the pot containing Collembola was mixed thoroughly, and 20 g of the subsamples was added to each M + C microcosm daily for 3 d. The average number of Collembola individuals in each microcosm was 16.66 ± 8.9 (1080 ± 8.9 ind m^{-2}), compared to natural densities of 707.1 ± 290 ind m^{-2} in the dry season and 1385.7 ± 339.9 ind m^{-2} in the rainy season [70]. During this period, the microcosms were maintained in the laboratory at 25 °C.

Three grams of fragmented or intact air-dried leaf litter from each tree species were placed in 9 cm × 9 cm litter bags with l mm