



Succession of soil microarthropod communities during the aboveground and belowground litter decomposition processes



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ABSTRACT

The process of litter decomposition is driven by interactions among climate, litter quality, and decomposers. However, information about the soil animal community involved in fine-root litter decomposition remains limited. We compared the composition of the soil microarthropods involved in leaf and root decomposition in field experiments using litterbags. To evaluate the relative effects of litter type and initial litter position, we set up a two-factor experiment (litter type \times litter position). Litterbags containing either roots or leaves were placed at two positions (either on the soil surface or buried within the soil) and were collected to follow the succession of microarthropods in the decomposing litter for three years. We found different successional patterns of soil microarthropods between the natural processes of leaf and root litter decomposition (i.e. leaves on the soil surface and roots buried within the soil), which were caused by taxonomy-specific responses to both litter quality and litter position. Prostigmata were clearly affected by the stage of litter decomposition; they were initial colonisers of decomposition in all litterbag treatments. The abundances of other taxa were more determined by litter position; however, Oribatida showed a preference for later stages of decomposition, while Collembola and Mesostigmata were strongly determined by water content related to litter position. Although litter quality was not the primary factor controlling their distribution, the ratio of Oribatida to Collembola gradually increased during the decomposition process in the belowground litterbags. Our results indicate that Oribatida are primarily involved in root litter decomposition process, particularly in the late stages of decomposition under natural conditions.

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1. Introduction

Plant litter decomposition is the most important biogeochemical process in the cycling of carbon and nutrients in terrestrial ecosystems, especially, forest ecosystems (Chapin et al., 2011). Previous studies suggest that the decomposition process is regulated by interactions among three factors: physicochemical environment (climate and soil environment), litter quality, and soil organisms (Swift et al., 1979; Lavelle et al., 1993). Although physicochemical environment (particularly climate) and litter quality are the predominant drivers of decomposition (Couteaux et al., 1995; Aerts, 1997; Cornwell et al., 2008), generalising the role of soil

organisms as decomposers remains difficult (Kampichler and Bruckner, 2009; Garcia-Palacios et al., 2013). The effects of soil organisms on decay rates are mostly lower than those of other factors and are often insignificant (Wall et al., 2008; Makkonen et al., 2012; Fujii et al., 2016a), which has reduced the focus on the roles of soil organisms. However, the greater part of effects of environment and litter quality on decomposition processes is realised through the activity of soil organisms; thus, soil decomposer communities should not remain a ‘black box’ and should be studied in detail (Wardle, 2002).

The contribution of fine roots to the decomposition process is crucial because fine roots are the primary source of organic matter input to the soil, with an input that is often equivalent to the input from leaf litter (Vogt et al., 1996; Norby et al., 2004). Although understanding of the litter decomposition process was biased towards leaf litter until recently (Berg and McClaugherty, 2008; Zhang et al., 2008), the number of studies comparing leaf and root decay processes has started to increase (Freschet et al., 2013).

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These studies tried to evaluate different patterns among leaf and root decomposition processes of various plant species with a special focus on litter traits (e.g., Hobbie et al., 2010; Freschet et al., 2012; Fujii et al., 2016b; Ma et al., 2016). However, there still exists a large uncertainty in our understanding, as some of patterns, such as different patterns of nutrient release during leaf and root decomposition, cannot be explained only by litter traits (Hobbie, 2015). This unsolved issue may be due in part to the lack of information about the decomposers of root litter. Although some studies measure the contributions of soil organisms to root decomposition rates (Parker et al., 1984; M. Judas et al., 1995; Fujii et al., 2016a; García-Palacios et al., 2016), the community composition of the decomposers that are actually involved in root decomposition processes remains to be determined (but see, Fujii and Takeda, 2012).

Soil microarthropods, such as springtails and mites, are the most abundant group of soil mesofauna in almost all terrestrial ecosystems, with densities that often reach hundreds of thousands of individuals per m² (Petersen and Luxton, 1982). Microarthropods contribute to the degradation of organic matter directly through litter consumption and comminution, or indirectly through stimulation of microbial activity by grazing (Hanlon, 1981; Seastedt, 1984; Coleman et al., 2004). The composition of soil microarthropod communities could be affected by the distinct litter quality of leaves and roots because different communities are sometimes organised on leaf litters of different species (Takeda, 1987). In addition, the different pathways of leaf and root litter inputs may affect soil microarthropod communities; whereas leaf decomposition begins on the soil surface and moves downwards as decomposition proceeds (i.e., with new additions of litter fall), root litter decomposition begins within the soil. This probably occurs because soil microarthropods are strongly controlled by the physical characteristics of microhabitats along a soil vertical profile (Ponge, 2000; Fujii and Takeda, 2012). Thus, we expect that the composition of the soil microarthropod community in root litter will be different from that in leaf litter because of these two differences (i.e. litter quality and position) in the processes of leaf and root decomposition.

In the present study, we compared the composition of soil microarthropods involved in leaf and root decomposition in field experiments using litterbags. To evaluate the relative effects of litter type and initial litter position on the successional changes in the composition of soil microarthropods during decomposition, we set up a two-factor experiment (litter type × litter position) and followed the succession of microarthropods (primarily, Oribatida, Collembola, Prostigmata and Mesostigmata) in decomposing litter for three years. Although Collembola and Oribatida are often grouped into the same trophic level and are considered to occupy similar niches in decomposition processes (Wallwork, 1970; Kaneko et al., 1995), the two groups differ in a variety of ecological traits that include mobility, productivity, level of predation pressure, and tolerance to abiotic conditions (Siepel, 1994; Maraun et al., 2003; Lindberg and Bengtsson, 2005). In particular, some oribatid species ingest recalcitrant woody substrates (Coleman et al., 2004), whereas Collembola often depend on labile carbon such as root exudates (Larsen et al., 2007; Endlweber et al., 2009; Fujii et al., 2016c). Therefore, for the effects of litter type, we hypothesised that Oribatida (rather than Collembola) would be primarily involved in the decomposition of root litter, which is a more recalcitrant substrate than leaf litter. For the effects of initial litter position, we hypothesised that the dominance ratio between Oribatida and Collembola would be different because Collembola are more sensitive than Oribatida to abiotic microhabitat conditions (Maraun et al., 2003; Lindberg and Bengtsson, 2005). For Prostigmata and Mesostigmata, which include predator species of

Collembola (Coleman et al., 2004), might depend on the dynamics of collembolan abundance.

2. Materials and methods

2.1. Site description

The study was conducted in a natural forest of *Chamaecyparis obtusa* (Cupressaceae) at the Kamigamo Experimental Forest Station of Kyoto University, approximately 12 km north of Kyoto City, Japan (35°04' N, 135°43' E). The study site is situated at the top of a gradual hill (200 m above sea level). The mean annual precipitation was 1416 mm and the mean temperature was 14.9 °C across the three years of the study period. The canopy layer of the forest consisted primarily of *C. obtusa*, and the understorey vegetation was composed of the shrubs *Cleyera japonica*, *Eurya japonica*, *Lyonia ovalifolia*, *Rhododendron macrosepalum*, and *C. obtusa* saplings. The soil humus form at the site was moder, with an organic layer (A₀) approximately 5 cm thick (approximately, L: 1–1.5 cm, F: 1–1.5 cm, H: 2–3 cm) above a poorly developed A horizon 1–2 cm thick, and a BC layer. In the A₀ layer, fine roots of *C. obtusa* were densely distributed and formed a root mat.

2.2. Experimental design

Litterbags were used to record changes in soil microarthropod communities during leaf and root decomposition (see Fujii and Takeda (2012) for details). Leaves and fine roots (≤ 2.0 mm diameter) of *C. obtusa* were collected at the study site. These litter substrates were air-dried to a constant weight at room temperature and then 2.0 g of each substrate was enclosed in 10 × 10 cm² 1-mm-mesh nylon bags. A 20 × 10 m² study plot was laid out and divided into 20 subplots of 5 × 2 m² each. 15 of the 20 subplots were used in this study; the other five subplots were not used because fallen logs covered them. In June 2007, we placed litterbags in the 15 subplots. We prepared two types of litterbag that contained either leaves or fine roots, and half of each type of bag was positioned above ground and the other half below ground, creating four litterbag treatments. Aboveground litterbags were secured with metal pins to prevent movement. Belowground litterbags were inserted into the A₀ + A layer at a 45° angle (about 7 cm depth) and anchored with metal pins. A total of 420 litterbags (four treatments × 15 subplots × seven sampling times) were prepared. Litterbags were collected in September and December 2007, March, June and December 2008, June 2009, and June 2010; on each sample date, 60 bags (four treatments × 15 subplots) were collected, placed in polyethylene bags, and transported to the laboratory.

2.3. Sample measurements

In the laboratory, we removed soil particles and living plant parts that had adhered to the surface of the litterbags and then weighed the wet mass of the litterbags. Soil animals in each litterbag were extracted using a Tullgren funnel at 35 °C for 5 days, and were identified and counted at the species level for Collembola and at the order or suborder level for the other taxa under an optical microscope at a magnification of 400 ×. After the extraction of soil animals, the litterbags were dried at 40 °C to a constant mass, and we weighed the dry mass of the litterbags and litterbag contents. Water content of the litterbags (Wc) was calculated as: $Wc = (A - B) / B \times 100$ (%), where A is the wet mass of bags and B is the dry mass of bags. The total C and N contents of the initial litter and of each sample were measured by drying at 70 °C, finely grinding in a laboratory mill, and then combusting (NC analyser SUMIGRAPH NC-900, Sumitomo Chemical Co., Osaka, Japan). The total C and N

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