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Impacts of soil fauna on lignin and cellulose degradation in litter decomposition across an alpine forest-tundra ecotone

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A B S T R A C T

The degradation of lignin and cellulose is the primary ecological process in terrestrial ecosystems; these chemical changes have been associated with the subsequent colonization and activity of decomposer flora and fauna. To evaluate the contribution of soil fauna on lignin and cellulose degradation during litter decomposition, we conducted a field experiment along an elevation gradient: coniferous forest, alpine timberline and alpine meadow, and monitored *Abies faxoniana* and *Rhododendron lapponicum* foliar litter decomposition with litterbags of different mesh sizes. We observed soil fauna significantly accelerated litter decay. Soil fauna effect on cellulose degradation rate was significantly accelerated in the snowing period (213-320d), which were 19.3%, 12.36%, 27.96% in *A. faxoniana* litter and 9.2%, 32.65%, 22.11% in *R. lapponicum* litter in the coniferous forest, alpine timberline and alpine meadow, respectively. By contrast, lignin degradation rates by soil fauna were higher in the later stages (321-554d). In addition, the average monthly contribution of soil fauna effect on cellulose degradation rate mainly occurred during the first year. However, the contribution of lignin degradation by soil fauna was higher in coniferous forest and alpine meadow, where they were 13.84% and 18.06% in *A. faxoniana*, and 14.5% and 10.1% in *R. lapponicum* litter. Elevation gradient and seasonal dynamics will influence on activity of soil fauna, which may modify the impacts of soil fauna on lignin and cellulose degradation during litter decomposition. Elucidating the role of soil fauna in litter decomposition is important for understanding the formation of soil organic matter in alpine ecosystems.

1. Introduction

Lignin is a recalcitrant component of litter substrate, and exerts considerable control over the rate of decomposition [1,2]. Cellulose is the most abundant biopolymer and polysaccharide in plant litter and typically constitutes 20–30% of plant litter mass [3]. The degradation of lignin and cellulose as a highly dynamic process that is critical for the cycling of terrestrial soil organic matter during decomposition [4,5]. Nevertheless, the current understanding of litter decomposition suggests that in alpine ecosystems, decomposition occurs slowly due to low temperatures, which leads to the accumulation of recalcitrant components in the litter horizon [6,7]. Decomposers may play an essential role in these ecosystem function, especially in the biogeochemical cycling [8,9]. Still, little information is available on how soil fauna across an alpine forest-tundra ecotone manipulate the processes of cellulose and lignin degradation during foliar litter decomposition. For instance, variation of litter lignin content appeared to be the predominant driver of decomposer community composition [10], and freeze-thaw cycle destroys the lignin structure of litter, which allows soil fauna and microbes to enter litter and accelerates decomposition rates in subarctic forested ecosystems [11].

At the global scale, climate and litter quality (i.e., chemical and physical composition) are considered the most important controlling factor litter decomposition, which can explaining approximately 60–70% of litter decomposition rates [12,13]. Additionally, soil biota (microbes and fauna) can explain the residual variance in global litter decomposition, and soil fauna consistently enhance litter decomposition at both global and biome scales [14]. The mechanisms used by soil fauna uses to decompose litter include substrate digestion and fragmentation, which indirectly increases surface and give microbes a big surface area to expedite feeding and inoculation [15,16]. In general, changes in phenolic and lignin concentrations during the early stages of decomposition can influence subsequent rates of decomposition at later stages, and environmental factors may interact with invertebrate

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abundance to influence rates of decomposition [17]. Simultaneously, low C:N ratios and low concentrations of polyphenolics also favor consumption by some invertebrate decomposers and can accelerate litter decomposition [6].

Average temperatures have risen globally over the past century, and temperature is widely considered the primary factor in treeline formation and maintenance, with the most pronounced and rapid changes occurring at high altitudes and latitudes. These ecosystems are characterized by a short growing season, low temperatures and low vegetation cover [8,18,19]. Empirical studies suggest that the most abundant litter decomposers in alpine pastureland are earthworms, millipedes, sciaridae and dipteran larvae, soil fauna diversity is essential for sustaining litter decomposition and for the stability of this service in alpine areas [20,21]. Moreover, winter snow cover maintains a relatively stable level of moisture and temperature, which provides a favorable environment for the survival and activity of soil fauna, as they are physically moving the litter into soil, thus allowing microbes to better access litter, the resultant stimulation of microbial growth has important implications for litter decomposition and lignin and cellulose degradation [9,22]. Further, seasonal frosts and freeze-thaw cycles not only directly affect litter decomposition rate and C release, but also damage refractory materials such as lignin and cellulose, and influence the activities of soil fauna rapidly initiates lignin and cellulose degradation [23,24].

The alpine forest-tundra ecotone responds more sensitively and rapidly to climate change than other terrestrial ecosystems [25,26], leading to alterations of plant community structure and species composition, and consequently of the plant litter decomposition [27]. In our previous studies, we have revealed that alpine meadow is a good habitat for Acarina, in contrast to coniferous and timberline forest that Collembola, Oribatida, Prostigmata and Mesostigmata were the dominant communities, and found that there were higher numbers of individuals and higher density of soil fauna in the alpine timberline [28–30]. Therefore, we hypothesize that soil fauna contribute more to lignin and cellulose degradation in timberline forest across the alpine forest-tundra ecotone. To test this hypothesis, a field experiment was conducted to investigate lignin and cellulose degradation rates of two dominant species (*Abies faxoniana* and *Rhododendron lapponicum*) at three elevations with litterbags of different mesh sizes (3 mm and 0.04 mm). The objectives of our study were: (1) to determine the impact of soil fauna on lignin and cellulose degradation in leaf litter decay, and (2) to determine the relationship between environmental factors and the contributions of soil fauna to the lignin/cellulose degradation rate across the alpine forest-tundra ecotone.

2. Materials and methods

2.1. Site description

The study was conducted at the long-term Research Station of Alpine Ecosystems located on Zhegu Mountain (longitude 102°41′32″ to 102°41′54″E, latitude 31°51′48″ to 31°51′53″N, approximately 3900–4200 m above sea level, with a notable vertical zonality) in the Miyaluo Nature Reserve in Li County, Sichuan Province, southwestern China. This reserve is in a transitional region between the Tibetan Plateau and the Sichuan Basin, where the watersheds of the Dadu River and Minjiang River are distributed [25]. The weather is cool in summer and cold in winter, and the annual mean air temperature range is approximately 6–12 °C. The absolute maximum and minimum air temperatures are 12.6 °C in July and −8 °C in January, respectively. The annual mean precipitation ranges from 600 to 1100 mm. The snow-covered season starts in November and lasts until the end of April (6–7 months) in the alpine zone. The dominant shrub species are *Berberis silva-taroucana* Schneid, *Lonicera lanceolata* L, *Rosa omeiensis* Rolfe, *Rhododendron taliense* Franch, and *Sorbus rufopilosa* Schneid. The major herbaceous plants are *Aconitum fangianum* W. T. Wang, *Agrostis hugoniana* Rendle, *Delphinium caeruleum* Jacq. ex Camb, *Deyeuxia scabrescens* Griseb, *Festuca wallichanica* E. Alexeev, *Pedicularis* davidii, *Polygonum sphaerostachyum* D. Don, and *Senecio winklerianus* H.M. Soil types are Cryumbreps and Histosols (United States Department of Agriculture Soil Taxonomy) in the coniferous forest and shrubland and in the alpine meadow, respectively. The alpine treeline is a transitional zone that is located near the upper elevational boundary of the coniferous forest, which is approximately 4000 m.

Fifty-meter-wide transects separated by more than 1 km were set perpendicularly to the contour line in the forest-tundra ecotone. The vegetation types in these three transects, in which permanent sample plots were established in 2008, vary from coniferous forest (3900–4000 m) to alpine shrubland (4000–4200) to alpine meadow (> 4200 m). The dominant tree species in the coniferous forest are Minjiang fir (*Abies faxoniana*) and alpine rhododendron (*Rhododendron lapponicum*). The forest understory is cold and wet, with thick layers of moss and humus. The height and coverage of woody shrubs decrease from the shrubland to alpine meadow. The shrubland is characterized by the presence of woody shrub species and long-lived herbaceous perennials.

2.2. Experimental design and sampling

The contribution of soil fauna to lignin and cellulose degradation was determined using the litterbag method with two different mesh sizes. In October 2012, freshly senesced leaves of conifers (*A. faxoniana*) and evergreen shrubs (*R. lapponicum*) were collected from the forest floor. To avoid structural damage during oven drying, the fresh litter was air-dried for over two weeks at room temperature. Samples weighing 10 g were placed in nylon litterbags (20 × 20 cm) with mesh sizes of 0.04 mm on the bottom and 0.04 mm (to exclude soil fauna) or 3.00 mm (to permit soil fauna) on top. Litter was spread as flat as possible to keep it in contact with the soil. Each litterbag was labeled with an aluminum number tag. Subsamples of the foliar litter from each species were oven-dried at 65 °C for 72 h to determine the quality and chemical composition (C, N, P, lignin, cellulose, and phenol concentrations) (Table 1).

A total of 216 litterbags (2 species × 2 mesh types × 3 elevations × 3replicates × 6 sampling dates) were placed on the forest-tundra ecotone. Button temperature loggers (iButton DS1921, Maxim/Dallas Semiconductor, Sunnyvale, CA, USA) were wrapped in plastic to protect them from water and were placed inside the litterbags to monitor the temperature every 3 h. Because of freezing and thawing processes, the selection of sampling dates were based on changes in freezing and thawing dynamics from previous field observations [31]. To quantify lignin and cellulose degradation during critical periods, we

Table 1
Initial foliar litter chemistry of the two species (mean ± SE, n = 3).

Species	C	N	P	Lignin	Cellulose	Phenol	C/N	Lignin/N
	(g kg^{-1})	(g kg^{-1})	(g kg^{-1})	(g kg^{-1})	(g kg^{-1})	(g kg^{-1})		
A. faxoniana	568.2 ± 26.2a	17.26 ± 0.65a	1.09 ± 0.06a	149.5 ± 4.3a	219.5 ± 9.2a	22.67 ± 0.78a	32.92 ± 2.15a	12.72 ± 7.68a
R. lapponicum	489.7 ± 4.0b	8.34 ± 0.04b	1.03 ± 0.03b	181.8 ± 20.6b	192.8 ± 49.5b	23.50 ± 0.80a	58.71 ± 3.10b	23.12 ± 24.31b

Different lowercase letters indicate a significant difference between species within the same variable at $P < 0.05$.