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Secondary compounds can reduce the soil micro-arthropod effect on lichen decomposition

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ABSTRACT

Phenolic compounds have been shown in several studies to have important 'carryover effects' on litter decomposition, microbial nutrient immobilization and nutrient availability. These effects arise in part because of the adverse effect they have on the feeding activities of litter-feeding invertebrates such as micro-arthropods that drive decomposition processes. However, the interactive effects of phenolic compounds and soil micro-arthropods on litter decomposition are poorly understood. Phenolic compounds can easily be removed by acetone rinsing from living lichens, allowing us to specifically test the role that phenolic compounds (and their removal) have in controlling the effects of micro-arthropods on the decomposition of their litter. We performed a litter-bag experiment aimed at exploring how lichen litter mass loss and nutrient release during decomposition was affected by phenolics (by using acetone rinsed and non-rinsed lichen material) and micro-arthropod activity (by using different mesh sizes to allow or exclude entry by micro-arthropods) for each of six contrasting lichen species (*Cladonia rangiferina, Cladonia stellaris, Evernia prunastri, Hypogymnia physodes, Pseudevernia furfuracea* and *Usnea dasypoga*). Both the removal of phenolic compounds and the presence of micro-arthropods accelerated mass and nutrient release overall, but not for either of the two *Cladonia* species. Removal of phenolics also had an overall positive effect on the effects of arthropods on the loss of P, but not mass and N, from the decomposing lichens. Further, for *U. dasypoga,* but not the other species, natural levels of phenolic compounds deterred micro-arthropods from accelerating mass loss, and the removal of these compounds enabled micro-arthropods to enhance its decomposition. Our findings that lichen phenolic compounds can sometimes interact with micro-arthropods to influence lichen litter mass loss and nutrient release during decomposition assists our understanding of how lichens and their consumers may impact on organic matter dynamics, biochemical nutrient cycling and other related ecosystem processes.

1. Introduction

Litter quality chemical characteristics such as concentrations of nutrients and secondary compounds have been long recognized as major drivers of the decomposability of plant litter (Swift et al., 1979; Cornwell et al., 2008). As such, plant phenolic compounds, which are carbon based secondary metabolites, have been shown in several studies to have important 'carryover effects' on microbial activity, decomposition, microbial nutrient immobilization and nutrient availability (Northup et al., 1995; Hättenschwiler and Vitousek, 2000; Cornelissen et al., 2004; Coq et al., 2010). Moreover, phenolic compounds may also decrease plant foliar palatability (Levin, 1976), and this can have important carryover effects on the decomposability of plant litter (Findlay et al., 1996). These effects arise in part because of the adverse effect they have on the feeding activities of soil invertebrates that can drive decomposition processes, such as micro-arthropods (Petersen and Luxton, 1982). However, the interactive effects of phenolic compounds and soil micro-arthropods on litter decomposition are poorly understood.

Lichens make up an important part of primary producer communities in many high altitude and high latitude environments worldwide (Matveyeva and Chernov, 2000). They also have a major role in many ecosystems through driving nutrient cycling, for example by capturing atmospheric nutrients, serving as a food source for primary consumers, and providing shelter for invertebrates (Knops et al., 1991, 1996; Nash, 2008). Factors driving

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lichen decomposition and thus the contribution of lichens to carbon and nutrient cycling are poorly understood, but recent studies have shown that lichen properties such as concentrations of thallus N and phenolic compounds are important drivers of lichen decomposition (Lang et al., 2009; Asplund and Wardle, 2013). A number of lichenivorous arthropods, such as Collembola and Acari, are often found in great numbers on lichens (Gerson and Seaward, 1977). However, whether these micro-arthropods play a role in driving lichen decomposition in the manner that has frequently been shown for plant litter decomposition (Petersen and Luxton, 1982; Schädler and Brandl, 2005; Joo et al., 2006) has so far not been experimentally tested.

A substantial proportion of the phenolic compounds present in lichens can be non-destructively extracted from living thalli with 100% acetone (Solhaug and Gauslaa, 1996, 2001). Using this technique, previous studies have shown that lichen phenolic compounds can deter various lichenivorous insects, gastropods and mammals (Gauslaa, 2005; Pöykkö et al., 2005; Asplund and Gauslaa, 2008; Nybakken et al., 2010). Further, we recently showed that removing phenolic compounds increases both the decomposability and palatability of thallus material for a number of lichen species of different growth forms and from contrasting habitats (Asplund and Wardle, 2013). The inhibitory effect of phenolic compounds on lichen decomposition may arise because of the antimicrobial activities of such compounds (Lawrey, 2009). As such, this technique provides the opportunity to study the combined effects of phenolic compounds and soil arthropods on mass and nutrient loss from lichens during the decomposition process.

We examined two key factors that may have a role in affecting the decomposition of lichen material, i.e., the presence of phenolics and of micro-arthropods, using six contrasting lichen species in a boreal forest in S Norway. We achieved this by performing a litter bag experiment involving material from each of the six species, in which we manipulated phenolic concentrations in the thalli (by using acetone rinsed and non-rinsed material) and micro-arthropod presence (by using different mesh sizes to allow or exclude entry by micro-arthropods). We sought to test the following two hypotheses: (i) Phenolic compounds in lichens will limit arthropod feeding activity, and removal of phenolics will therefore cause an enhancement of the invertebrate effect on thallus mass loss and nutrient release during decomposition; and (ii) the influence of phenolic compound removal on this invertebrate effect will vary across contrasting lichen species, and will be greater for those species that have the highest concentrations of phenolic compounds. By addressing these hypotheses we aim to advance our understanding of the role that micro-arthropods and lichen phenolic compounds have in driving key ecosystem processes known to be driven by lichens in boreal forest ecosystems.

2. Materials and methods

2.1. Lichen material and study site

The study site was a mixed *Picea abies* forest, at Kollåsen (Ski, SE Norway 59°45′N, 10°56′E), with feather mosses dominating the forest floor and *Cladonia* spp. dominating rock outcrops. The climate is suboceanic, with 1020 mm of precipitation during 2012 (Thue-Hansen and Grimenes, 2013). For this study we chose to work with six common boreal forest species – two ground-dwelling: *Cladonia stellaris*, *Cladonia rangiferina*, and four epiphytic: *Evernia prunastri*, *Hypogymnia physodes, Pseudevernia furfuracea* and *Usnea dasypoga* (Table 1). For each species, we collected approximately 50 g of fresh material in April 2012. The material was immediately brought to the laboratory where the thalli were rinsed from debris and left to air-dry before being stored at −18 °C until the start of the experiments (Honegger, 2003). Fresh lichen material was used because most lichen species do not produce senesced litter, but rather the litter falls to the ground following fragmentation without the chemical composition of the litter being altered; decomposition therefore begins when the litter is more or less fresh. For this reason most previous studies on lichen decomposition have used living material (Coxson and Curteanu, 2002; Caldiz et al., 2007; Campbell et al., 2010; Asplund and Wardle, 2013). In contrast Lang et al. (2009) attempted to induce lichen senescence by incubating moist lichens in darkness and subsequently freezing the thalli in liquid N_2, but they noted that even this procedure could not guarantee complete tissue death and that this treatment may have produced additional artefacts.

2.2. Removal of phenolic compounds and chemical analyses

Phenolic compounds were reduced in concentration using acetone, a standard procedure commonly applied to lichens (e.g. Solhaug and Gauslaa, 1996, 2001; Gauslaa, 2005; Pöykkö et al., 2005; Asplund et al., 2010). Acetone does not enter the membranes of desiccated cells, and phenolic compounds are deposited extracellularly and can thus be extracted from dry lichens without detrimental side effects (Solhaug and Gauslaa, 2001). For each species, half of the air-dried material was placed in excess acetone for three 20 min intervals following Solhaug and Gauslaa (1996).

Table 1
Characteristics of the studied species, including medullary (M) and cortical (C) phenolic compounds, the initial nitrogen (N), phosphorous (P) and phenolic compound concentration, and extraction efficiency of phenolic compounds.

		N (%)	P (%)	Phenolic concentration (%)				Extraction efficiency (%)	
				Controls		Acetone rinsed		M	C
				M	C	M	C		
Cladonia rangiferina	M: Fumarprotocetraric acid, C: atranorin	0.35	0.013	2.48	0.79	0.13	0.25	94.6	68.8
Cladonia stellaris	M: Perlatolic acid, C: usnic acid	0.38	0.009	0.18	1.85	0.005	0.054	97.1	97.1
Evernia prunastri	M: Evernic acid, C: atranorin, chloroatranorin, usnic acid	0.70	0.038	3.29	2.94	0.015	0.86	99.6	70.6
Hypogymnia physodes	M: Protocetraric, physodic, physodalic acids, C: atranorin, chloroatranorin	0.56	0.039	10.28	2.11	0.19	1.82	98.1	13.8
Pseudevernia furfuracea	M: Oxyphysodic and physodic acids, C: atranorin, chloroatranorin	0.66	0.011	6.15	9.86	0.27	0.73	95.6	92.6
Usnea dasypoga	M: Salazinic acid, C: usnic acid	0.60	0.017	0.72	3.14	0.06	1.36	91.7	56.6