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Fungal depsidones – an inducible or constitutive defence against herbivores in the lichen *Lobaria pulmonaria*?

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Abstract

Herbivore-deterrent depsidones in the epiphytic lichen *Lobaria pulmonaria* were quantified after a 104-day exposure to indigenous lichen-feeding mollusc communities in broadleaved deciduous forests in southeastern Norway. Controls and acetone-rinsed living thalli were transplanted under open and shaded tree canopies. Rinsed thalli had their depsidone concentration reduced to 36% of the pre-rinsing level, which is below the level needed to deter grazing molluscs. Grazing did not raise the concentration of depsidones beyond the level occurring in control to which molluscs had no access. Inducible responses were not detected in controls nor in acetone-rinsed thalli. Depsidone resynthesis was negligible in acetone-rinsed thalli regardless of grazing and/or light regimes. Our results suggest that C-based depsidones represent a constitutive type of herbivore defence in *L. pulmonaria*. A constitutive defence is probably an advantage for stress-tolerant slow-growing lichens inhabiting habitats with a constant presence of generalist invertebrate herbivores.

Zusammenfassung

Bei der epiphytischen Flechte *Lobaria pulmonaria* wurde das herbivorenabschreckende Depsidon quantifiziert, nachdem die Flechten 104 Tage indigenen flechtenfressenden Schneckengesellschaften in breitblättrigen Laubwäldern im südöstlichen Norwegen ausgesetzt waren. Sowohl die Kontrollen als auch mit Aceton gespülte lebende Thalli wurden in offene und schattige Kronendächer versetzt. Die gespülten Thalli besaßen eine Depsidonkonzentration, die auf 36% der ursprünglichen Konzentration vermindert war, was unterhalb des Gehalts liegt, der notwendig ist, um weidende Schnecken abzuschrecken. Die Beweidung erhöhte die Konzentration des Depsidons nicht über den Gehalt hinaus, der in den thalli vorkam, zu denen die Schnecken keinen Zugang hatten. Induzierbare Reaktionen konnten weder bei den Kontrollen noch bei den acetongespülten Thalli festgestellt werden. Die Depsidon-Resynthese war bei den acetongespülten Thalli unabhängig von der Beweidung oder vom Beleuchtungsgrad vernachlässigbar. Unsere Ergebnisse lassen vermuten, dass kohlenstoffbasiertes Depsidon einen grundlegenden Typ der Herbivorenabwehr bei

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L. pulmonaria darstellt. Eine grundlegende Abwehr ist möglicherweise ein Vorteil für stresstolerante, langsam wachsende Flechten, die Habitate bewohnen in denen unspezifische, invertebrate Herbivoren dauerhaft anwesend sind.

Keywords: Acetone rinsing; Invertebrate; Molluscs; Plant–herbivore interaction; Slugs; Snails; Stictic acid

Introduction

Lichens are long-lived and stress-tolerant organisms in habitats where plants often are less abundant. Such organisms depend on a strong herbivore defence or have a low nutritional value. Lichens produce a variety of secondary compounds (Huneck & Yoshimura, 1996). A number of medullary compounds have been shown to deter grazing (Gauslaa, 2005; Lawrey, 1983; Reutimann & Scheidegger, 1987; Pöykkö, Hyvärinen, & Backor, 2005; Gauslaa, 2005; Reutimann & Scheidegger, 1987). Chemical defences can either be expressed facultatively, i.e. induced by an environmental cue (e.g. herbivory), or constitutively, i.e. present all the time (Karban & Baldwin, 1997). Inducible defences, which are generally considered more cost effective, are widely studied in vascular plants (Tallamy & Raupp, 1991; e.g. Karban & Baldwin, 1997). However, the significance of grazing as a possible regulating mechanism for secondary lichen compounds is not well known. Nybakken and Julkunen-Tiitto (2006) found no effect of artificial reindeer grazing on the concentration of several medullary depsidones in three mat-forming *Cladonia* species under laboratory conditions. The induction of secondary chemistry by oribatid mites was indirectly evidenced in *C. bacilliformis* and *C. norvegica*; (Timdal, 1989; see photos of *C. norvegica* at http://www.toyen.uio.no/botanisk/lav/). In these two species the red rhodocladonic acid was exclusively synthesised around cavities formed by the mites on the lower side of basal squamules.

Experimental studies testing possible quantitative changes of secondary chemistry in lichens induced by natural grazing are rare. This study focuses on the epiphytic old forest lichen *Lobaria pulmonaria* (L.) Hoffm. In calcareous broadleaved forests, where lichen-feeding molluscs are frequent, *L. pulmonaria* can be limited by mollusc grazing (Scheidegger, 1995; Asplund & Gauslaa, 2008). This lichen has high concentrations of medullary depsidones, and these were neither influenced by light conditions nor by variations in growth rates in two recent field transplantation experiments (McEvoy, Gauslaa, & Solhaug, 2007; Nybakken, Asplund, Solhaug, & Gauslaa, 2007). At the same time, the content per area of these compounds increased with increasing thallus size at a juvenile stage (Asplund & Gauslaa, 2007), indicating some responsiveness. Recent grazing experiments using acetone rinsed and control thalli of *L. pulmonaria* in the laboratory (Gauslaa, 2005), as well as in the field (Asplund & Gauslaa, 2008), showed that a reduction of contencentraion of depsidones by acetone rinsing significantly increased the grazing damage by lichen-feeding molluscs. Resynthesis of secondary compounds in lichens has already been studied in a few lichens subjected to acetone rinsing, such as *Xanthoria elegans*, *X. parietina* and *Xanthoparmelia somloensis*, but with a focus to test sun-screening functions of cortical compounds (Solhaug & Gauslaa, 1996; Nybakken, Solhaug, Bilger, & Gauslaa, 2004; McEvoy, Nybakken, Solhaug, & Gauslaa, 2006). UV-B induced the synthesis of sun-screening cortical compounds (parietin and usnic acid) in these studies, and artificial addition of photosynthates boosted their resynthesis (Solhaug & Gauslaa, 2004; McEvoy et al., 2006). The removal of sun-screening secondary compounds in *X. parietina* did not result in increased grazing in subsequent grazing experiments (Gauslaa, 2005). *Lobaria pulmonaria* with herbivore-deterrent extractable depsidones is a promising species for experiments testing the inductive power of grazing on medullary compounds in acetone-rinsed thalli.

In this study we use *L. pulmonaria* transplants from an experiment designed to quantify mollusc grazing in deciduous forests (Asplund & Gauslaa, 2008). Acetone-rinsed *L. pulmonaria* thalli, low in depsidones, and controls were transplanted to forests with high populations of lichen-feeding molluscs. By using a factorial design ($\pm$acetone rinsing, $\pm$mollusc exclosure, two light levels) and quantifying the depsidones at the end of the transplantation, we aimed to search for factors, or combinations of factors, which may regulate the synthesis of secondary compounds occurring in *L. pulmonaria*.

Our main hypothesis is that natural mollusc grazing increases the resynthesis of secondary compounds in *L. pulmonaria*. Earlier experiments using artificial grazing (Nybakken & Julkunen-Tiitto, 2006) may have failed to induce secondary compound synthesis because of lacking chemical signals, e.g. from the regurgitate of the herbivore (Arimura, Kost, & Boland, 2005). A constitutive defence is assumed to be common under resource-limiting conditions (Herms & Mattson, 1992; Van Zandt, 2007). Among lichens, *L. pulmonaria* has a high growth rate (Gauslaa, Lie, Solhaug, & Ohlson, 2006; Gauslaa et al., 2007), and is hardly N-limited due