



# Carbon-based secondary compounds in the lichen *Hypogymnia physodes* deter detritivorous woodlice



Paul Christian Wieners<sup>a</sup>, Wolfgang Bilger<sup>a</sup>, Yngvar Gauslaa<sup>b,\*</sup>

<sup>a</sup> Christian-Albrechts-University, Botanisches Institut, Abt. Ökophysiologie der Pflanzen, Am Botanischen Garten 3-9, D-24118 Kiel, Germany

<sup>b</sup> Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway

## ARTICLE INFO

### Article history:

Received 10 May 2017

Received in revised form

14 October 2017

Accepted 2 November 2017

Corresponding Editor: Peter D. Crittenden

### Keywords:

Carbon-based secondary compounds

Chemical defense

Grazing preference

*Hypogymnia physodes*

Isopods

Lichenivory

Lichens

Macrodetritivores

*Porcellio scaber*

Woodlouse

## ABSTRACT

Woodlice are not widely recognized as lichen-feeding invertebrates. We sought to discover whether the woodlouse, *Porcellio scaber*, could feed on the lichen *Hypogymnia physodes* and if the lichen carbon-based secondary compounds CBSCs would reduce grazing. We cut lichen thalli in two pieces, one was non-destructively rinsed in acetone to remove CBSCs; the other served as a control. Both pieces were fed to woodlice in a choice experiment. The CBSC concentration of individual thalli ranged from 3 to 19%. The woodlice grazed all pieces, but preferred the acetone-rinsed pieces, depending on the amount of CBSCs present in the non-extracted counterpart. The woodlice were not deterred from feeding on samples with CBSC concentrations  $\leq 5\%$ , which corresponded to natural contents in shade-adapted thalli. This suggested that *P. scaber* tolerates this amount of compounds at least in the short-term. In conclusion, *P. scaber* can feed on *H. physodes*, but CBSCs deter them from feeding.

© 2017 Elsevier Ltd and British Mycological Society. All rights reserved.

## 1. Introduction

Lichens are well defended against generalist herbivores by carbon-based secondary compounds (CBSCs) also called lichen compounds (Gauslaa, 2005; Pöykkö et al., 2005; Cernajová and Svoboda, 2014). Such compounds are particularly abundant in lichens from oligotrophic, N-deficient habitats. In contrast, most N-fixing cyanolichens are deficient in CBSCs (Gauslaa, 2005), but may produce N-based defence compounds such as microcystins (e.g. Kaasalainen et al., 2012).

A unique feature of lichens is that a major part of their CBSC pools can be extracted non-destructively by 100% acetone from living, desiccated lichens (Solhaug and Gauslaa, 2001; Candotto Carniel et al., 2017) without affecting N and P contents or other intracellular compounds (Pöykkö et al., 2005; Asplund and Wardle, 2013). This is because lichen CBSCs are deposited outside fungal

hyphae, and because 100% acetone is unable to penetrate through dry cell walls, and so does not enter the living parts of desiccated tissues. Our selected lichen, *Hypogymnia physodes*, has high total mean CBSC concentration (often  $>9\%$  of dry matter, DM; Solhaug et al., 2009). Its major medullary CBSCs are physodalic and physodic acids, which may reach a concentration of  $>20\%$  of DM. The minor CBSCs ( $<1\%$  of DM) are the medullary protocetraric acid and the cortical atranorin/chloroatranorin (Solhaug et al., 2009).

Woodlice, isopod crustaceans belonging to the mainly terrestrial suborder Oniscidea, are among the most abundant macrodetritivores in temperate forests (Zuo et al., 2014). These invertebrates are common in shaded parts of forests with dead wood (Topp et al., 2006; Purchart et al., 2013). While some species have developed trachea-like lungs, most have gills and therefore depend on high air humidity. Thus they live a hidden and nocturnal life, but are seen during moist cloudy weather on e.g. the lower part of epiphyte-covered tree trunks inside forests. There, they often hide underneath bark pieces, lichen and bryophyte mats during daylight hours (Y. Gauslaa, pers. obs.). Being detritivores, woodlice eat fungal tissues

\* Corresponding author.

E-mail address: [yngvar.gauslaa@nmbu.no](mailto:yngvar.gauslaa@nmbu.no) (Y. Gauslaa).

and algae (Crowther et al., 2011; Crowther and A'Bear, 2012; A'Bear et al., 2014). However, apart from a few anecdotal reports on lichen feeding (Richardson, 1975, p 154, Gerson and Seaward, 1977), they have not been considered among the lichen feeding invertebrates.

In the present study we used the woodlouse species *Porcellio scaber*, a common macroarthropod in temperate forests, also in the more nutrient poor oak and pine forests (De Smedt et al., 2016) where *H. physodes* is abundant. It is the most common woodlouse in Norway, being found in drier sites (Sutton, 1972), and is particularly common at forest edges (De Smedt et al., 2016). Our aim was to test whether *P. scaber* avoids *H. physodes* thalli with high CBSC concentrations as do lichenivorous gastropods, insects and mammals (Gauslaa, 2005; Pöykkö et al., 2005; Nybakken et al., 2010). We also aimed to quantify the minimum CBSC concentration needed to deter woodlice grazing.

## 2. Materials and methods

*H. physodes* was collected 5 August 2016 from all sides of *Picea abies* trunks at and near north-facing forest edges bordering an agricultural landscape in southeastern Norway, Akershus, 59°39'43" N, 10°50'40" E, 140 m a.s.l. Here, the studied woodlouse was often seen on the ground in humid weather (Y. Gauslaa, pers. obs.). Solhaug et al. (2009) have documented a strong positive relationship between diffuse light and CBSC content in *H. physodes*. To ensure a variation in CBSC concentration in our experimental thalli, we sampled lichens from forest edges with substantial small-scale variation in the open sky exposure and thus a high variation in diffuse light. Thalli were air dried at room temperature, taken to Kiel, Germany, and within 5 d stored at -18 °C until the start of experiments. The first experiment was conducted September 6–20, 2016, the second comprised a sequence of trials done during a university teaching course from mid-October 2016 to early February 2017.

The woodlouse used in both experiments, *P. scaber*, was originally collected under stones in the Botanical Garden of the Christian-Albrechts-University, Kiel, N Germany 54°20'46.76" N, 10°06'58.23" E, 21 m above sea level, and a population maintained since 2011 in a terrarium where they were fed with food for fish (Pond Sticks, Tetra GmbH, Melle, Germany).

Air-dried frozen thalli of *H. physodes* were cut into two similar-sized pieces of roughly 110 mg (70–190 mg; min-max size for individual pieces) and weighed (AW224, Sartorius, Göttingen, Germany; accuracy  $d = 0.1$  mg). Two slightly different extraction protocols were used for the lichens used in the two experiments. The first experiment employed the extraction protocol of Solhaug et al. (2009). One piece from each pair was rinsed 4 times in 10 ml acetone for 30 min each. In the second experiment the thalli were extracted twice in 10 ml acetone for 20 min.

After extraction, thalli were reweighed; the non-extracted piece from each thallus was the control. Each of these rinsed-control pairs was fixed with white cotton thread onto a filter paper (diameter 90 mm) and put into a Petri dish. After thoroughly moistening the filter paper and the lichen thalli with distilled water, we added five woodlice in each Petri dish. The Petri dishes were closed and stored in a dark room at 23 °C for 24 h. A Petri dish with five woodlice and the extracted and control portion of the lichen sample is shown before (Fig. 1A) and after 24 h grazing (Fig. 1B). The lichen pieces at the end of the experiment were oven-dried at 60 °C to constant mass and weighed again. Grazing was estimated as mg grazed dry matter (DM)  $d^{-1}$  for each lichen piece, and is an estimate of the total grazing by the five woodlouse individuals. Grazing preference (%) for the extracted piece of each thallus pair was computed as  $(\text{rinsed DM}_{\text{grazed}} \times 100) / (\text{rinsed DM}_{\text{grazed}} + \text{control DM}_{\text{grazed}})$ .

In the first experiment, the extracts of each extraction step for each thallus were pooled in a Falcon tube (Sarstedt, Nümbrecht, Germany). After evaporation of the acetone, the residue was dissolved in 40 ml methanol (HPLC grade, Roth, Karlsruhe, Germany). After appropriate dilution, the absorbance of the solutions was determined with a spectrophotometer (Uvikon 922, Kontron Instruments, Milano, Italy).

To compare the effects of the different times and the slightly different extraction protocols, we used one-way ANOVAs for: (1) the percent extracted CBSCs; (2) grazed mass of controls; (3) grazed mass of extracted thalli; and (4) grazing preference of extracted thalli, after checking homoscedasticity and normality. The two last parameters were log-transformed to meet the ANOVA requirements. We used a linear multiple regression model for predicting grazed biomass after extracting the CBSCs. Explanatory variables were percent extracted CBSCs and grazed biomass of control pieces. In the text, means  $\pm 1$  standard error are given; error bars in Figs show 1 standard deviation. We ran all statistical analyses in SigmaPlot (Systat Software, San Jose, CA).

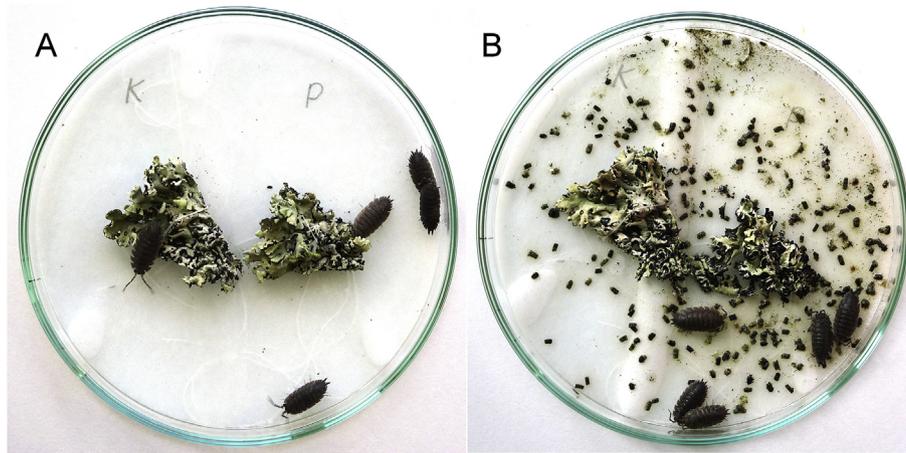
## 3. Results

The greater grazing of extracted versus control lichen pieces was evident by eye in many of the trials (Fig. 1). The distribution of the feces often indicated a longer time spent by the woodlice near the extracted piece. The woodlice fed on all lichen layers, but particularly on the upper cortex, the photobiont layer and the upper part of the medulla (Fig. 1B). More than 88% of the 311 pairs in both experiments had more grazing in rinsed pieces than in controls. However, every control thallus from both experiments had some grazing, even those with the highest CBSC concentrations (total range in grazing of controls: 0.3–38.1 mg  $d^{-1}$ ).

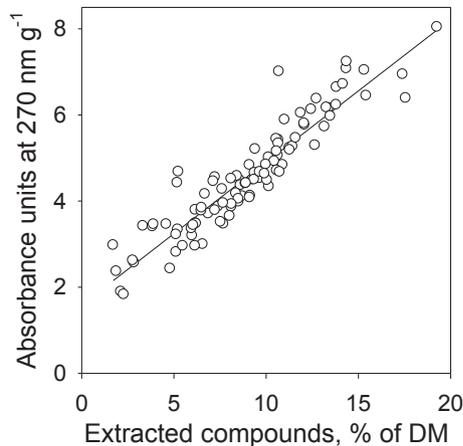
The close relationship between the absorbance units at 270 nm per DM and the percent extracted material ( $r^2_{\text{adj}} = 0.864$ ;  $P < 0.001$ ; Fig. 2) supported the view that the percent mass loss during rinsing represented the CBSC concentration in the lichens. The CBSC concentration varied substantially between experimental pairs (total range: 1.6–19.3%;  $n = 310$ ). The percent extracted material from extracted pieces did not significantly differ between the two experiments (ANOVA; data not shown); the total mean extraction was  $9.6 \pm 0.2\%$  of DM. The thalli used in the first experiment were slightly, but significantly ( $P < 0.001$ ) larger (total thallus size including both pieces:  $246.2 \pm 4.6$  mg) than those used in the second experiment ( $218.2 \pm 1.1$  mg). However, there were no significant correlations between thallus size and percent extraction, either between thallus size and consumed DM of extracted pieces or with respect to control pieces. For these reasons, the two experiments were combined in the plots and statistical analyses.

The mean grazing preference for acetone-rinsed thalli was  $63.6 \pm 0.7\%$  ( $n = 310$ ; total range 37.5–99.4%) with no difference between the two experiments (Fig. 3; insert). Grazing preference increased significantly with the percent extracted compounds (Fig. 3). The regression line crossed the 50% grazing preference at approximately 4.3% CBSC-concentration, implying that CBSC concentrations lower than approximately 4–5% are insufficient to deter the woodlouse *P. scaber*. The total grazed biomass for both pieces combined in each pair did not significantly change with extracted compounds (linear regression analysis;  $r^2_{\text{adj}} = 0.007$ ;  $P = 0.069$ ).

The grazed DM of control pieces (total mean  $18.8 \pm 0.4$  mg DM  $d^{-1}$ ;  $n = 310$ ; equivalent to  $3.8$  mg  $d^{-1}$  woodlouse $^{-1}$ ) did not differ between the two experiments (Fig. 4A; insert), but declined significantly with increasing CBSC concentration from approximately  $30$  mg  $d^{-1}$  ( $= 6$  mg  $d^{-1}$  woodlouse $^{-1}$ ) at the lowest natural CBSC concentration to just 1–2 mg  $d^{-1}$  in the samples with the



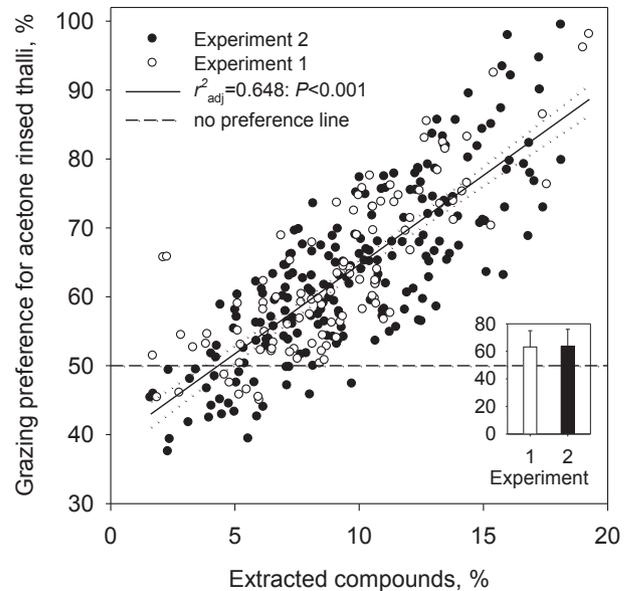
**Fig. 1.** Photos of the same Petri dish with the lichen *Hypogymnia physodes* at the start (A) and the end (B) of 24 h grazing by five specimens of the woodlouse species *Porcellio scaber*. The Petri dish shows a pair of an acetone-rinsed (the piece at the right side of the dish) and a control piece (at left side) of one *H. physodes* thallus.



**Fig. 2.** The relationship between absorbance units measured at 270 nm per dry mass (DM) and the weighed mass loss in percent of DM during acetone-extraction of lichen carbon-based secondary compounds ( $r^2_{adj} = 0.864$ ;  $P < 0.001$ ;  $n = 100$ ).

highest CBSC concentration of 19% (Fig. 4A). As for the grazing preference (Fig. 3), grazed DM of lichens (Fig. 4A, B) showed completely overlapping ranges and variation between thalli used in the two experiments.

The grazed DM of acetone-rinsed pieces with hardly any CBSCs left (total mean  $33.3 \pm 0.6 \text{ mg DM d}^{-1} = 6.7 \text{ mg d}^{-1} \text{ woodlouse}^{-1}$ ) was at similar levels in both experiments (Fig. 4B; insert). Grazing of rinsed lichens strongly increased in those samples that had contained a high CBSC concentration before extraction (Fig. 4B). The regression between rinsed DM consumed and percent CBSC before rinsing (Fig. 4B) was significantly improved after adding grazed biomass of the control counterpart as an additional explanatory parameter in a multiple regression model (Table 1). This was done because the grazed DM of controls and of extracted pieces were just weakly correlated ( $r = -0.234$ ); the low variance inflation factors (VIF; Table 1) showed that multicollinearity was not a problem in the multiple regression. For the extracted thalli that had the lowest CBSC concentration before extraction (Fig. 4B), grazing was at a similar level ( $\approx 30 \text{ mg d}^{-1} = 6 \text{ mg d}^{-1} \text{ woodlouse}^{-1}$ ) as in the control pieces with the lowest natural compound concentration (Fig. 4A). This was consistent with the lack of preference (Fig. 3) at low concentrations of CBSCs. With increasing removal of CBSCs, grazing by the five woodlice increased to

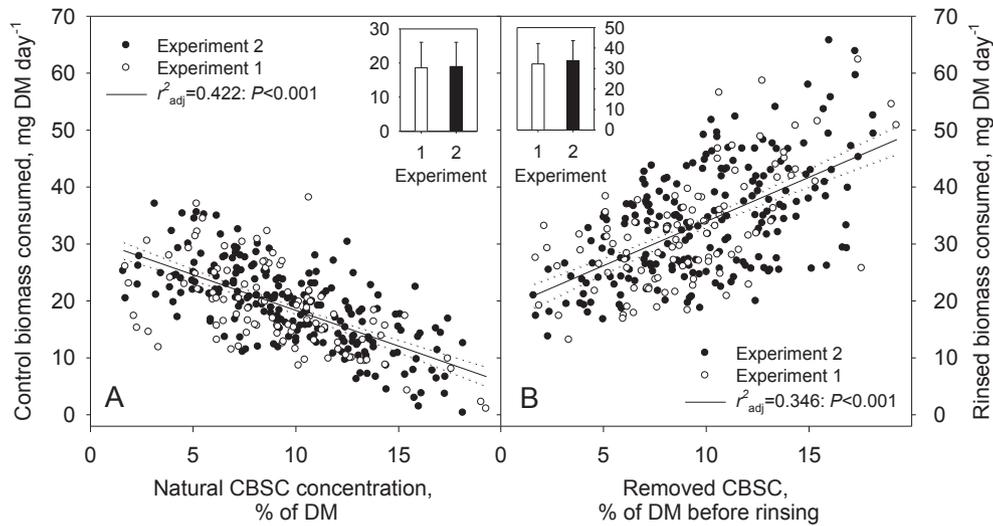


**Fig. 3.** The relationship between the grazing preference for CBSC-deficient *Hypogymnia physodes* thalli and the extracted CBSCs. Grazing preference was recorded after 24 h grazing by five specimens of the woodlouse species *Porcellio scaber*. The solid line shows the regression line, the dotted lines show 95% confidence intervals, and the hatched line shows the no-preference line. Filled and open symbols represent two separate experiments done in the same way, but separated in time and run by different persons. The insert shows the overall mean grazing preference for CBSC-deficient thalli in each of these two experiments, vertical bars show 1 standard deviation.

$\approx 50 \text{ mg d}^{-1}$  even for the thalli that had the highest CBSC concentration (19%) before the start (Fig. 4B), equivalent to a consumption of  $10 \text{ mg d}^{-1} \text{ woodlouse}^{-1}$ .

#### 4. Discussion

This study confirms the old and often forgotten experiments of Stahl (1904) who showed that woodlice actually grazed lichens after their CBSCs had been reduced by a sodium carbonate solution treatment. An acetone extraction is better than the soda solution extraction because acetone causes less damage to the lichen (Solhaug and Gauslaa, 2001, 2004). The CBSCs in *H. physodes* are not highly detrimental to woodlice as these compounds do not reduce grazing preference unless the total concentration is higher than



**Fig. 4.** The relationships between (A) the consumed dry mass of control thalli and their concentration of CBSC, and (B) between the consumed dry mass of acetone-rinsed pieces and the concentration of CBSC that had been removed by the rinsing. Each pair of control and rinsed pieces of *Hypogymnia physodes* had been served to five specimens of the woodlouse species *Porcellio scaber* for 24 h. The solid line shows the regression line; the dotted lines show 95% confidence intervals. Filled and open symbols represent two separate experiments done in the same way, but separated in time and run by different persons. The inserts show the overall mean grazed DM in control thalli (insert in A) and the overall mean grazed DM in CBSC-deficient thalli (insert in B) in each of these two experiments, vertical bars show 1 standard deviation.

**Table 1**

Multiple regression model for the grazed lichen biomass in extracted lichen pieces using (1) the CBSC concentration prior to extraction and (2) the grazed biomass of their control counterparts as explanatory variables. Grazed lichen biomass in extracted lichen pieces =  $7.475 + (0.355 * \text{grazed control biomass}) + (1.997 * \% \text{ extracted CBSC})$ ; ( $r^2_{\text{adj}} = 0.383$ ;  $P < 0.001$ ;  $n = 310$ ).

|                        | Coefficient $\pm$ 1SE | T      | P      | VIF   |
|------------------------|-----------------------|--------|--------|-------|
| Constant               | 7.475 $\pm$ 2.761     | 2.707  | 0.007  |       |
| Grazed control biomass | 0.355 $\pm$ 0.080     | 4.420  | <0.001 | 1.735 |
| % extracted CBSC       | 1.997 $\pm$ 0.155     | 12.893 | <0.001 | 1.735 |

VIF: Variance inflation factor.

4–5% (Fig. 3). This is consistent with a quantitative rather than a qualitative defense (e.g. Smilanich et al., 2016). The natural concentration in thalli collected from interior parts of shaded spruce forests (6.7%; see Solhaug et al., 2009) is just slightly above this limit, implying a risk for lichens growing in the shade to be consumed by woodlice.

We consider the DM loss during acetone rinsing to be a good estimate of total CBSC concentration in *H. physodes* for the following reasons: (1) In an HPLC-study of CBSCs in *H. physodes* from five nearby habitats, the mean concentration was  $9.5 \pm 0.4\%$  ( $n = 75$ ; with a total range of 3.6–20.8%) (Solhaug et al., 2009). These values correspond well with the mass loss measured after our extraction ( $9.6 \pm 0.2\%$ ; 1.6–19.3%;  $n = 310$ ). (2) There is a strong, positive relationship between the absorbance of extracts at 270 nm per DM and percent reduction in DM after the efficient acetone rinsing (Fig. 2). (3) Other studies have shown that extraction protocols similar to ours extract nearly all medullary CBSCs present (>97%) in *H. physodes* from intact, unground lichen material (McEvoy et al., 2006; Asplund et al., 2015). Because medullary CBSCs in general represent a much stronger herbivore defense than cortical compounds, which function mainly as solar radiation screens (as reviewed by Solhaug and Gauslaa, 2012), the reduced extraction of the minor cortical CBSCs (McEvoy et al., 2006) is unlikely to influence the grazing preference.

It is remarkable that *P. scaber* consistently ate, to some extent, even control thalli with high CBSC concentration (Fig. 4A), despite being known to discriminate between diets made up with different

microbe species (Ihnen and Zimmer, 2008) or diets with and without cadmium addition (Zidar et al., 2005). One interpretation is that there is a balance between the fodder quality and deterrence in woodlice feeding on CBSC-containing *H. physodes*. The strong increase in grazing of acetone-rinsed CBSC (Fig. 4B) is consistent with a hypothesis that investment by the lichen in CBSC-production increases in thalli with the highest nutrition quality. Future experiments should investigate this aspect.

An unusually diverse microflora is associated with the cuticle of the hindgut of *P. scaber* (Kostanjsek et al., 2002) and this may help to degrade toxic CBSCs. Oxidation of phenolics in the gut of *P. scaber* appears mainly due to the endosymbiotic bacteria of the hepatopancreas (Zimmer, 1999). Indeed, CBSC-degrading microbes have been isolated from the digestive organs of specialized lichenivores such as reindeer (Sundset et al., 2008, 2010).

Woodlice may contribute to the lack of *H. physodes* on shaded lower trunks in broadleaved deciduous stands. *P. scaber* prefers habitats with subneutral soil pH-ranges (VanStraalen and Verhoef, 1997), and declines with acidification (Zimmer and Topp, 1997). *H. physodes* is uncommon on trunks of trees growing in subneutral soils, but is more common on trunks on acidic soils. This is consistent with woodlouse-exclusion of *H. physodes* on lower parts of trees. Woodlice populations are predicted to increase with global warming (David and Handa, 2010) with possible more serious effects on lichens in the future.

In forests, a substantial biomass of epiphytic lichens falls to the ground as litter (Esseen, 1985; Knops et al., 1996; Berryman and McCune, 2006; Caldiz and Brunet, 2006). Epiphytic lichen litter thus feeds a decomposer community (Asplund and Wardle, 2017). Consumption and decomposition of *H. physodes* litter on the forest floor is fast, and acetone rinsing of the lichen litter speeds up decomposition rates (Asplund et al., 2013; Asplund and Wardle, 2013). Detritivores may thus contribute to rapid nutrient cycling by decomposing litter from epiphytic lichen communities. Considering the high woodlice feeding also of lichens rich in CBSCs (Fig. 4), macroinvertebrates likely affect lichen litter pools on the forest floor.

Hyvärinen et al. (2000) found that somatic parts of *H. physodes* have lower concentration of CBSCs than soralia which increase in

abundance as thalli grow. The lack of relationship between sampled thallus size and CBSC concentration in our data set, suggests that all studied specimens had reached the mature reproductive stage.

In conclusion, the macrodetritivorous woodlice *P. scaber* responded like other lichenivorous organisms by increasing their lichen consumption after non-destructive extraction of lichen CBSCs with acetone. However, their preference for CBSC-deficient lichens was lower than that of earlier studied lichen-feeding specialists. *H. physodes* from shade-adapted habitats had a lower CBSC concentration than that required to deter the woodlice, suggesting that woodlice could be important consumers of lichens on the lower parts of tree trunks.

## Acknowledgments

We thank Dr. Marko Rohlfs for pointing out woodlice as test organisms. We are grateful to the students who did the measurements in experiment 2 during their course “biol 106 Ecology and Evolution” in winter semester 2016/17. Thanks also to Knut Asbjørn Solhaug for preparing Fig. 1 and to four anonymous reviewers for useful and constructive comments.

## References

- A'Bear, A.D., Boddy, L., Kandeler, E., Ruess, L., Jones, T.H., 2014. Effects of isopod population density on woodland decomposer microbial community function. *Soil Biol. Biochem.* 77, 112–120.
- Asplund, J., Bokhorst, S., Kardol, P., Wardle, D.A., 2015. Removal of secondary compounds increases invertebrate abundance in lichens. *Fungal Ecol.* 18, 18–25.
- Asplund, J., Bokhorst, S., Wardle, D.A., 2013. Secondary compounds can reduce the soil micro-arthropod effect on lichen decomposition. *Soil Biol. Biochem.* 66, 10–16.
- Asplund, J., Wardle, D.A., 2013. The impact of secondary compounds and functional characteristics on lichen palatability and decomposition. *J. Ecol.* 101, 689–700.
- Asplund, J., Wardle, D.A., 2017. How lichens impact on terrestrial community and ecosystem properties. *Biol. Rev.* 92, 1720–1738.
- Berryman, S., McCune, B., 2006. Estimating epiphytic macrolichen biomass from topography, stand structure and lichen community data. *J. Veg. Sci.* 17, 157–170.
- Caldiz, M.S., Brunet, J., 2006. Litterfall of epiphytic macrolichens in *Nothofagus* forests of northern Patagonia, Argentina: relation to stand age and precipitation. *Austral Ecology* 31, 301–309.
- Candotto Carniel, F., Pellegrini, E., Bove, F., Crosera, M., Adami, G., Nali, C., Lorenzini, G., Tretiach, M., 2017. Acetone washing for the removal of lichen substances affects membrane permeability. *Lichenologist* 49, 387–395.
- Cernajová, I., Svoboda, D., 2014. Lichen compounds of common epiphytic Parmeliaceae species deter gastropods both in laboratory and in Central European temperate forests. *Fungal Ecol.* 11, 8–16.
- Crowther, T.W., A'Bear, A.D., 2012. Impacts of grazing soil fauna on decomposer fungi are species-specific and density-dependent. *Fungal Ecol.* 5, 277–281.
- Crowther, T.W., Jones, T.H., Boddy, L., 2011. Species-specific effects of grazing invertebrates on mycelial emergence and growth from woody resources into soil. *Fungal Ecol.* 4, 333–341.
- David, J.F., Handa, I.T., 2010. The ecology of saprophagous macroarthropods (millipedes, woodlice) in the context of global change. *Biol. Rev.* 85, 881–895.
- De Smedt, P., Wuyts, K., Baeten, L., De Schrijver, A., Proesmans, W., De Frenne, P., Ampoorter, E., Remy, E., Gijbels, M., Hermy, M., Bonte, D., Verheyen, K., 2016. Complementary distribution patterns of arthropod detritivores (woodlice and millipedes) along forest edge-to-interior gradients. *Insect Conservation Divers.* 9, 456–469.
- Esseen, P.A., 1985. Litter fall of epiphytic macrolichens in two *Picea abies* forests in Sweden. *Can. J. Bot.* 63, 980–987.
- Gauslaa, Y., 2005. Lichen palatability depends on investments in herbivore defence. *Oecologia* 143, 94–105.
- Gerson, U., Seaward, M.R.D., 1977. Lichen-invertebrate associations. In: Seaward, M.R.D. (Ed.), *Lichen Ecology*. Academic Press, London, pp. 69–119.
- Hyvärinen, M., Koopmann, R., Hormi, O., Tuomi, J., 2000. Phenols in reproductive and somatic structures of lichens: a case of optimal defence? *Oikos* 91, 371–375.
- Ihnen, K., Zimmer, M., 2008. Selective consumption and digestion of litter microbes by *Porcellio scaber* (Isopoda : Oniscidea). *Pedobiologia* 51, 335–342.
- Kaasalainen, U., Fewer, D.P., Jokela, J., Wahlsten, M., Sivonen, K., Rikkinen, J., 2012. Cyanobacteria produce a high variety of hepatotoxic peptides in lichen symbiosis. *Proc. Natl. Acad. Sci. U. S. A.* 109, 5886–5891.
- Knops, J.M.H., Nash III, T.H., Schlesinger, W.H., 1996. The influence of epiphytic lichens on the nutrient cycling of an oak woodland. *Ecol. Monogr.* 66, 159–179.
- Kostanjšek, R., Štrus, J., Avguštin, G., 2002. Genetic diversity of bacteria associated with the hindgut of the terrestrial crustacean *Porcellio scaber* (Crustacea: Isopoda). *Fems Microbiol. Ecol.* 40, 171–179.
- McEvoy, M., Nybakken, L., Solhaug, K.A., Gauslaa, Y., 2006. UV triggers the synthesis of the widely distributed secondary compound usnic acid. *Mycol. Prog.* 5, 221–229.
- Nybakken, L., Helmersen, A.M., Gauslaa, Y., Selås, V., 2010. Secondary compounds restrain lichen feeding by bank voles (*Myodes glareolus*). *J. Chem. Ecol.* 36, 298–304.
- Purchart, L., Tuf, I.H., Hula, V., Suchomel, J., 2013. Arthropod assemblages in Norway spruce monocultures during a forest cycle - a multi-taxa approach. *For. Ecol. Manag.* 306, 42–51.
- Pöykkö, H., Hyvärinen, M., Bäckor, M., 2005. Removal of lichen secondary metabolites affects food choice and survival of lichenivorous moth larvae. *Ecology* 86, 2623–2632.
- Richardson, D.H.S., 1975. *The Vanishing Lichens*. David & Charles, Newton.
- Smilanich, A.M., Fincher, R.M., Dyer, L.A., 2016. Does plant apparency matter? Thirty years of data provide limited support but reveal clear patterns of the effects of plant chemistry on herbivores. *New Phytol.* 210, 1044–1057.
- Solhaug, K.A., Gauslaa, Y., 2001. Acetone rinsing - a method for testing ecological and physiological roles of secondary compounds in living lichens. *Symbiosis* 30, 301–315.
- Solhaug, K.A., Gauslaa, Y., 2004. Photosynthates stimulate the UV-B induced fungal anthraquinone synthesis in the foliose lichen *Xanthoria parietina*. *Plant Cell Environ.* 27, 167–176.
- Solhaug, K.A., Gauslaa, Y., 2012. Secondary lichen compounds as protection against excess solar radiation and herbivores. *Prog. Bot.* 73, 283–304.
- Solhaug, K.A., Lind, M., Nybakken, L., Gauslaa, Y., 2009. Possible functional roles of cortical depsides and medullary depsidones in the foliose lichen *Hypogymnia physodes*. *Flora* 204, 40–48.
- Stahl, G.E., 1904. *Die Schutzmittel der Flechten gegen Tierfrass*. Pages 357–375 *Festschrift zum siebzigsten Geburtstag von Ernst Haeckel*. Gustav Fischer, Jena.
- Sundset, M.A., Barboza, P.S., Green, T.K., Folkow, L.P., Blix, A.S., Mathiesen, S.D., 2010. Microbial degradation of usnic acid in the reindeer rumen. *Naturwissenschaften* 97, 273–278.
- Sundset, M.A., Kohn, A., Mathiesen, S.D., Præsteng, K.E., 2008. *Eubacterium rangiferina*, a novel usnic acid-resistant bacterium from the reindeer rumen. *Naturwissenschaften* 95, 741–749.
- Sutton, S., 1972. *Woodlice*. Pergamon Press, Oxford, New York.
- Topp, W., Kappes, H., Kulfan, J., Zach, P., 2006. Distribution pattern of woodlice (Isopoda) and millipedes (*Diplopoda*) in four primeval forests of the Western Carpathians (Central Slovakia). *Soil Biol. Biochem.* 38, 43–50.
- VanStraalen, N.M., Verhoef, H.A., 1997. The development of a bioindicator system for soil acidity based on arthropod pH preferences. *J. Appl. Ecol.* 34, 217–232.
- Zidar, P., Bozic, J., Štrus, J., 2005. Behavioral response in the terrestrial isopod *Porcellio scaber* (Crustacea) offered a choice of uncontaminated and cadmium-contaminated food. *Ecotoxicology* 14, 493–502.
- Zimmer, M., 1999. The fate and effects of ingested hydrolyzable tannins in *Porcellio scaber*. *J. Chem. Ecol.* 25, 611–628.
- Zimmer, M., Topp, W., 1997. Does leaf litter quality influence population parameters of the common woodlice, *Porcellio scaber* (Crustacea: Isopoda)? *Biol. Fertil. Soils* 24, 435–441.
- Zuo, J., Fonck, M., van Hal, J., Cornelissen, J.H.C., Berg, M.P., 2014. Diversity of macrodetritivores in dead wood is influenced by tree species, decay stage and environment. *Soil Biol. Biochem.* 78, 288–297.