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Short Communication

Do lichen secondary compounds play a role in highly specific fungal parasitism?

Sonia MERINERO[a,b,*], Massimo BIDUSSI[b], Yngvar GAUSLAA[b]

[a]Universidad Rey Juan Carlos, Área de Biodiversidad y Conservación, E-28933 Móstoles, Madrid, Spain
[b]Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, PO Box 5003, N-1432 Ås, Norway

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ABSTRACT

Chemical interactions between highly host-specific lichenicolous fungi and their lichen hosts have been little studied. In an allometric study, we quantified carbon-based secondary compounds (CBSCs) in a mixed natural *Lobarina scrobiculata* population (N = 147) of the normal and the stictic acid-deficient chemotypes, both with and without galls of *Plectocarpon scrobiculatae*. We assessed the correlation between the presence/abundance of parasite galls and the lichen CBSCs contents, and quantified size-dependent contents of CBSCs. The parasite produced galls similarly in both chemotypes, indicating that the stictic acid complex does not deter *Plectocarpon*. Within both chemotypes, thalli with *Plectocarpon* had half the contents of all individual CBSCs than those without galls. There was a significant size-dependent increase in CBSC contents in thalli without galls, but not in those with. This study shows that lichen chemistry is involved in highly host-specific fungal parasitism, and widens our knowledge of specialized biotrophic fungal interactions.

Introduction

Lichenicolous fungi, inhabiting lichens, comprise ≈1 500 parasites differing in specialization and virulence (Hawksworth, 1982; Lawrey and Diederich, 2003). Low-virulent, highly specialized lichenicolous fungi are biotrophic mycoparasites because their ecological niche is restricted to healthy specific hosts for long periods (Mendgen and Hahn, 2002; Lawrey and Diederich, 2003). However, relationships between highly specialized lichenicolous fungi and their hosts are rarely studied. Mechanisms regulating host specificity could be related to chemical traits, but we do not know to what extent secondary chemistry regulates these associations (Lawrey and Diederich, 2003).

Most lichens produce carbon-based secondary compounds (CBSCs; Huneck and Yoshimura, 1996). Medullary CBSCs often

* *Corresponding author*. Universidad Rey Juan Carlos, Área de Biodiversidad y Conservación, E-28933 Móstoles, Madrid, Spain. Tel.: +34 914888288.
E-mail addresses: sonia.merinero@gmail.com, sonia.merinero@urjc.es (S. Merinero).
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deter grazers (e.g. Asplund et al., 2010; Solhaug and Gauslaa, 2012), whereas cortical ones mainly serve as sunscreens (Solhaug and Gauslaa, 2012). CBSCs may also deter microbes and lichenicolous fungi (Lawrey, 1989). In some cases, lichenicolous fungi cannot overcome the lichen's defense, and they only degrade lichen tissues after CBSC extraction (Lawrey, 1993, 2000). Moreover, some lichens inhibit growth of relatively specialized lichenicolous fungi (Lawrey, 1993). However, CBSC may not necessarily deter lichenicolous fungi because virulent generalist parasites degrade CBSCs (e.g. lecanoric acid), facilitating other parasites (see Torzilli et al., 1999; Lawrey, 2000). Specialized lichenicolous fungi may enhance their growth when inoculated on their frequent host (Lawrey, 1993), suggesting that specialized lichen parasites tolerate and/or overcome the defense of their main host. Thus, lichenicolous fungi with different degrees of specialization vary in their responses to CBSCs. Yet, relationships between highly host-specific lichenicolous fungi and their hosts' CBSCs are poorly known.

We focus on the parasite-host system comprising the cyanolichen *Lobarina scrobiculata* (Lobariaceae, Ascomycota) and its highly specialized lichenicolous fungus *Plectocarpon scrobiculatae* (Roccellaceae, Ascomycota; Fig. S1). The host occurs across the Northern Hemisphere and in oceanic parts of Africa, Australia, New Zealand and South America (Smith et al., 2009), whereas its parasite only occurs in Europe, Macaronesia and North America (Ertz et al., 2005). *Plectocarpon* forms basally constricted galls resembling lichen apothecia and reproduces mainly sexually (Ertz et al., 2005; Fig. S1). The relationship is likely commensalistic, because the parasite does not cause visual damage apart from local deformation due to gall induction (Hawksworth, 1982; Ertz et al., 2005). Its host produces the sun-screening cortical usnic acid (Solhaug and Gauslaa, 2012), the herbivore-deterrent medullary stictic acid complex and meta-scrobiculin (Gauslaa, 2008; Asplund et al., 2010). However, a chemotype lacking the stictic acid complex occurs in Alaska and Norway (Holien and Hilmo, 1991).

Here we compare CBSC contents in two *L. scrobiculata* chemotypes with and without *P. scrobiculatae* galls. Because lichen CBSC contents may increase with lichen size (Asplund and Gauslaa, 2007), a range of thallus sizes, with and without galls were sampled. Given the high specialization of *Plectocarpon* for one host, we hypothesize that lichen CBSCs do not constitute a defense against *Plectocarpon*. Our specific hypotheses are: (1) CBSC contents are similar and size-dependent in thalli with and without *Plectocarpon* galls; (2) the parasite forms galls in both chemotypes; and (3) the abundance of parasite galls, a surrogate of the parasite reproductive effort, does not correlate with the lichen CBSC contents.

Methods

Lobarina scrobiculata was collected on *Picea abies* in boreal rainforests at Foss, Nord-Trøndelag, Norway (see Hilmo et al., 2013 for details on the study area and sampling), from 29 intact branches (2–13 m from the ground) from 21 trees randomly collected in June 2011, the season with peak values of CBSCs in *L. scrobiculata* (Gauslaa et al., 2013). Branches with air-dried lichens were stored at −20 °C until extraction of CBSCs. All *L. scrobiculata* thalli with *P. scrobiculatae* galls were gathered from these branches. For each thallus with galls, one thallus of similar size without *P. scrobiculatae* galls was also randomly sampled from the same tree. Mean height on the tree for both categories did not differ (7.0 ± 3.6 and 6.8 ± 4.4 m for the thalli without galls and the ones with galls, respectively; ANOVA; $P > 0.05$). Size varied from 0.23 to 124.5 cm^2 with no difference between thalli with and without galls (n = 78 and 69, respectively; ANOVA, $P = 0.95$). The dry mass of each thallus was assessed, and the CBSCs extracted and

Table 1 – Mean lichen size and carbon-based secondary compound (CBSC) contents (±SE) of *Lobarina scrobiculata* with and without galls of *Plectocarpon scrobiculatae* for the normal and stictic deficient-chemotypes. Sample size for each category in brackets.

Lichen parameter	*Normal chemotype*			*Deficient chemotype*		
	Without galls (54)	With galls (62)	*P*	Without galls (15)	With galls (16)	*P*
Thallus area (cm^2)	13.99 ± 2.65	12.86 ± 2.55	0.759	11.57 ± 3.69	19.14 ± 5.90	0.287
Thallus dry mass (mg)	204.2 ± 42.2	200.0 ± 49.6	0.949	146.6 ± 52.1	236.7 ± 75.69	0.336
Specific thallus mass (mg cm^{-2})	12.08 ± 0.42	12.20 ± 0.37	0.825	11.26 ± 0.66	11.93 ± 0.37	0.388
CBSC (g m^{-2}):						
Usnic acid (cortical compound)	1.17 ± 0.12	0.64 ± 0.06	**0.000**	1.35 ± 0.28	0.49 ± 0.06	**0.009**
Meta-scrobiculin	1.64 ± 0.23	0.67 ± 0.09	**0.000**	2.21 ± 0.41	1.15 ± 0.18	**0.031**
Stictic acid complex, in total	4.05 ± 0.52	1.96 ± 0.19	**0.000**			
Constictic acid	1.01 ± 0.14	0.43 ± 0.05	**0.000**			
Cryptostictic acid	0.34 ± 0.04	0.17 ± 0.02	**0.000**			
Methyl norstictic acid	0.02 ± 0.00	0.01 ± 0.00	**0.042**			
Norstictic acid	0.06 ± 0.01	0.04 ± 0.01	0.277			
Stictic acid	2.63 ± 0.34	1.31 ± 0.13	**0.000**			
Total medullary compounds	5.69 ± 0.62	2.64 ± 0.25	**0.000**			
Total compounds	6.86 ± 0.72	3.28 ± 0.28	**0.000**	3.55 ± 0.58	1.65 ± 0.19	**0.006**

Significant *P*-values ($P < 0.05$) for differences between the two groups in bold (ANOVA).