

IMPORTANCE OF LICHEN SECONDARY PRODUCTS IN FOOD CHOICE OF TWO ORIBATID MITES (ACARI) IN AN ALPINE MEADOW ECOSYSTEM

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Abstract—In an alpine meadow ecosystem in the Swiss National Park, the lichens *Cetraria islandica* and *Cladonia symphylicarpa* occur in small vegetation patches dominated by *Carex firma* (Cyperaceae) and *Sesleria coerulea* (Gramineae). Laboratory food-choice experiments with two oribatid mites *Fuscozetes setosus* and *Carabodes intermedius* show that the thallus structure and secondary products of *C. islandica* are repellent factors against herbivorous mites. In contrast, secondary products of *C. symphylicarpa* may be an attractant for the mites.

Key Words—Lichen, herbivores, secondary products, oribatid mites, Acari, food choice, *Cetraria islandica*, *Cladonia symphylicarpa*, *Fuscozetes setosus*, *Carabodes intermedius*.

INTRODUCTION

The aim of this study was to investigate the influence of lichen secondary products on the food choice of two mite species, *Fuscozetes setosus* (C.L. Koch, 1841) and *Carabodes intermedius* Willmann, 1951, in an alpine meadow ecosystem in the Swiss National Park.

This meadow, 2550 m above sea level [vegetation type *Caricetum firmae* (Kerner) Br.-Bl.1926] has been studied since 1976 by a team of ecologists. A description of the study site is given by Matthey et al. (1981).

In this habitat, lichen phytomass accounts for only 1.1–5.5% of total phytomass (Galland, personal communication). The most abundant lichen species are *Cetraria islandica* (Iceland moss) and *Cladonia symphylicarpa*. The first spe-

cies is associated with *Carex firma* (Cyperaceae) and *Sesleria coerulea* (Gramineae) living in small vegetation patches without soil contact, while the second species grows on the edge of the vegetation cluster on disturbed humous subsoil.

About 50 species of oribatid mites occur in the habitat. Of these, 14 fed regularly on lichens, particularly on *C. symphycarpa*. In contrast, *C. islandica* was strictly avoided by all mite species. Two mite species, *F. setosus* and *C. intermedius*, the most active feeders on thalli of *C. symphycarpa* were chosen for food choice experiments. They were also the mite species most easily maintained in the laboratory. Both species belong to the panphytophagous feeding group (after Luxton, 1972). Whereas *F. setosus* is a dominant species that occurs regularly distributed in all vegetation types (Rohrer and Reutimann, 1984), *C. intermedius* was found predominantly associated within the small lichen microhabitats.

METHODS AND MATERIALS

The secondary products of both lichen species were identified by thin-layer chromatography (Culberson and Ammann, 1979). In *Cladonia symphycarpa*, the depside atranorin occurs in the cortex, the depsidone norstictic acid, as well as an unidentified substance occurring in the medulla. In the medulla of *Cetraria islandica* protolichenesterinic acid, an aliphatic lichen acid, as well as the depsidone fumarprotocetraric acid (a bitter substance) have been found (Culberson, 1969; Culberson et al., 1977).

The secondary products of freshly collected thalli of *C. symphycarpa* and *C. islandica* were extracted in acetone up to four times for a period of approx. 20 min each time. Thalli subjected to extraction constituted the substrate types B and G for food choice experiments (Figure 1). Other extracted thalli were then impregnated with the soluble secondary products of the respective species (repeated submersion of the thalli in acetone and desiccation in a thermal cupboard) (substrate types C and F).

The above-mentioned soluble secondary products were also applied on cellulose-free filter paper (diameter 10 mm, Balston Ltd) (substrate types D and E). Traces of secondary products were still detected in thalli B and G after three extractions. Lichenological spot tests (color reaction on lichen after application of an indicator solution) showed, however, typical discoloration of the inoculated lichen material on thalli C and F. Untreated desiccated thalli were used as controls (A and H).

The following eight substrate types were used in dual combinations for food-choice experiments with the mites: A, *C. islandica*, thalli, freshly collected, dried (control); B, *C. islandica*, thalli, with most secondary products

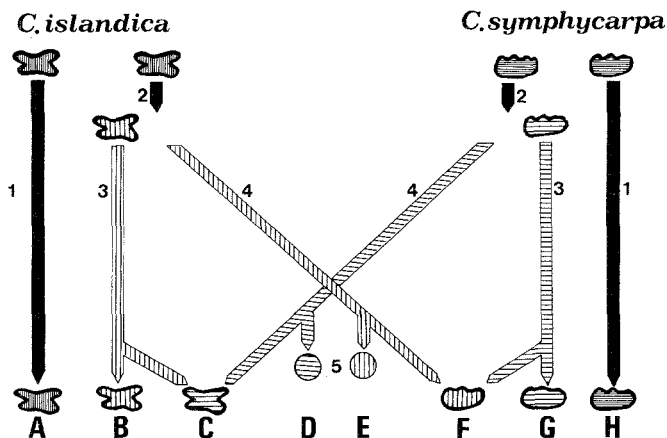


FIG. 1. Diagram of treatments: (1) no treatment, (2) acetone extractions of secondary products, (3) thalli subjected to acetone extractions, (4) acetone-soluble secondary products for impregnations, (5) disks of filter paper with secondary products dissolved in acetone. For further explanation, see text.

removed by acetone extractions; C, *C. islandica*, thalli, treated as in B, but with the secondary products of *C. symphycarpa*, applied in acetone solution; D, *C. islandica*, acetone-extracted secondary products on glass filter paper; E, *C. symphycarpa*, acetone-extracted secondary products on glass filter paper; F, *C. symphycarpa*, thalli, treated as in E, but with the secondary products of *C. islandica* applied in acetone solution; G, *C. symphycarpa*, thalli, with most secondary products removed by acetone extractions; and H, *C. symphycarpa*, thalli, freshly collected, dried (control).

Feeding experiments were conducted in covered glass dishes, 48 mm in diameter, containing substrate made of a mixture of plaster of Paris and charcoal (15:1) and with a relative humidity of 90–99%. In each dish, two of the eight food types (A–H, see above), were offered. Five adults of each species were used in each experiment. Seven pairwise combinations were chosen for the experiments (see Table 1 and Figure 1). The animals were kept at 20°C and observed once a day for a period of 6–19 days. Preferences in each pairwise combination were tested for with chi-square tests for goodness of fit (Wonnacott and Wonnacott, 1977). The null hypothesis (no preference) was that mites would be distributed equally between the two substrates. Observations of distribution on substrates were made once daily. Preferences were scored by summing the individual daily observations for the 6–19 days of each experiment. Feeding observations, feeding marks on the substrates, or fecal pellets were recorded as well.

Table 1. Results of Food-Choice Experiments with 7 Binary Combinations offered to *Fuscozetes setosus* and *Carabodes intermedius*^a

	<i>F. setosus</i>							<i>C. intermedius</i>						
	1	2	3	4	5	6		1	2	3	4	5	6	
A-H	7	0:11	H	H	H	<0.05		13	0:27	H	H	H	<0.001	
D-E	6	0:9	E			<0.05		9	0:0					
A-B	6	0:15	B		B	<0.01		6	0:24	B		B	<0.001	
C-H	17	0:26	H		H	<0.001		16	1:27	H		H	<0.001	
C-G	12	9:20	G			<0.01		17	6:31	G		G	<0.001	
G-H	6	4:5	H			<0.5		19	15:31	H	H	H	<0.0001	
B-G	9	2:20	G	G	B, G	<0.01		13	2:9	G	G	B, G	<0.05	

^a(1) number of controls, (2) number of individuals on the two substrates, (3) preferred substrate, (4) substrates on which feeding was directly observed, (5) substrates on which feeding marks and fecal pellets were observed, (6) values of *P* (chi-square tests).

RESULTS

The individuals of both species were repeatedly observed to eat thallus tissue of *Cladonia*. They strictly refuse untreated *Cetraria* (A and H, Table 1). Both species prefer to feed on untreated *Cladonia* even in the presence of *Cetraria* impregnated with *Cladonia* substances (C and H). This indicates a preference for *Cladonia* as substrate.

Carabodes significantly prefer untreated *Cladonia* to *Cladonia* without lichen substances (G and H). *Cetraria* with a reduced concentration of lichen substances are only eaten by *Fuscozetes* (A and B). No feeding attempts were noticed on the glass filter paper. When lichen products were nearly completely removed, lichen thalli of both species were eaten by both *Fuscozetes* and *Carabodes* (B and G).

Examination of gut contents show that both species digest only hyphae of lichen fungi and excrete lichen algae undigested. In laboratory experiments, unicellular green algae (unidentified) are only eaten by *Carabodes* (Reutimann, 1985).

DISCUSSION

Carabodes clearly avoids lichen substances on filter paper, where *Fuscozetes* reacts positively to the *Cladonia* lichen substances (atranorin, norstictic acid, and an unidentified substance) (D and E). Secondary products from *Cladonia* are an important factor leading to acceptance of *Cladonia* by *Fuscozetes*. They seem to have only a limited antiherbivore function against the two mite species (cf. Rundel, 1978). The distal sensory organs of the mite would perceive these compounds in the case of direct contact with the substrate by means of the chemosensory setae on the distal segments of legs I and II as well as the palpi (Krantz, 1978), but the compounds seem to lack a decisive stimulating quality in eliciting feeding behavior.

Lichen substances of *Cetraria* (protolichenesterinic acid, fumarprotocetraric acid) have, on the other hand, a certain repellent effect on these two mite species. The presence of appreciable concentrations of fumarprotocetraric acid (Culberson et al. 1977) might be responsible for this. Various authors report that reindeer avoid *Cladonia* species with fumarprotocetraric acid, whereas they eat species not containing it (Rundel, 1978). In contrast to *Cetraria islandica*, *Cladonia symphycarpa* does not contain these substances (Culberson, 1970; Culberson et al., 1977).

The different reactions of the two mite species to lichens may be seen in the context of other differences in feeding behavior. While both species are classified as panphytophagous feeders (after Luxton, 1972), *Fuscozetes* also captures living (and dead) animal prey (zoophagous and necrophagous feeding

subtype, after Luxton 1972; Reutimann, 1985). It is a relatively active species, unlike *Carabodes*, which seems to be a relatively inactive, predominantly fungivorous species. Patterns of spatial distribution in the habitat showed that *Carabodes* is closely associated with lichens (Reutimann, 1985). *Cladonia* thalli in alpine meadows often show traces of feeding of the type made by these mites.

In addition, *Carabodes* proved to be very constant in its substrate preferences for lichen in laboratory tests with different organic materials (Reutimann, 1985). Lichen-mite associations have been found repeatedly by various authors (e.g., Bellido, 1975; Andre, 1975; Gjelstrup and Søchting, 1979; see Seyd and Seaward, 1984, for a comprehensive view).

A main consequence of the acetone treatment is the abrupt death of the fungal and algal cells in the lichen thalli caused by lysis of the plasmalemmas. In addition, the traces of lichen substances remaining in the thalli B, C, F, and G show that the method should be improved upon for further experimental work. The efficiency of extraction could perhaps be increased with other solvents.

Relatively few studies have documented the ecological importance of lichen products in relation to herbivorous animals. A few lichen products have antibiotic effects. Lichens with certain lichen products (bitter constituents, protocetraric acid, fumarprotocetraric acid) are avoided by a few lichen-eating invertebrates (Gerson and Seaward, 1977). It is not exactly known in individual cases if secondary products ensure effective protection against consumption. Gerson and Seaward (1977) argued that various secondary products do not greatly influence the consumption of lichens.

Lawrey (1983) suspects that secondary products may be only one of several factors affecting food preferences of lichen herbivores. The quality of food may be diminished by a lower concentration of essential nutrients. In this connection the nature of the algal symbiont may be of importance. Lichens with the nitrogen-fixing bluegreen algae may have higher nitrogen contents. The symbiont in the case of the lichens examined in this study is a green alga. Our experiments show definitely that thallus structure is another important factor in mite feeding preferences. The relative importance of secondary products and other factors influencing food preferences may vary among lichen species. These species may be expected to differ in secondary product concentrations. Species with high growth rates, for example, may be able to compensate for herbivore damage, and there may be less selection for antiherbivore defense in these species.

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