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Surfactants in the Gut Fluids of *Porcellio scaber* (Isopoda: Oniscidea), and their Interactions with Phenolics

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Fluids from the gut lumen of *Porcellio scaber* showed significantly reduced surface tension compared to a buffer solution. Tests with several dilutions indicated that the concentration of the surface active substances (surfactants) was about 80-fold higher than the 'critical micelle concentration'. Phenolics, e.g. gallotannins, when ingested in the diet increased the surface tension of the gut fluid, indicating reduced concentrations of free surfactants. The significance of gut surfactants in *P. scaber*, their role in digestive processes, and their interaction with tannins in this saprophagous soil arthropod are discussed. © 1997 Elsevier Science Ltd. All rights reserved

Terrestrial isopods Decomposition Gut detergency Tannins Phenolics

INTRODUCTION

Tannins are naturally occurring water-soluble polyphenolic compounds capable of forming complexes with proteins (e.g. Haslam, 1979; Swain, 1979). Due to their capability of precipitating proteins *in vitro*, they have been assumed to play an important role in plant–herbivore interactions by reducing the digestibility of ingested plant tissue through the precipitation of ingested proteins or digestive enzymes (e.g. Feeny, 1976; Rhoades and Cates, 1976; Swain, 1979). However, in the gut lumen of phytophagous insects protein precipitation is unlikely to occur (Bernays, 1981; Martin and Martin, 1983). Alkalinity of gut fluids may protect proteins from binding by tannins (Berenbaum, 1980; Martin and Martin, 1983; Schultz and Lechowicz, 1986). Reducing gut conditions may prevent the generation of phenolic oxidation products (Appel and Martin, 1990) that are though mainly to precipitate proteins (Appel, 1993). Surface active detergents (surfactants) in gut fluids interfere in tannin–protein precipitation (Martin and Martin, 1984; Martin *et al*., 1985). Detergency may even be a more effective counteraction than gut alkalinity (Martin *et al*., 1985). Moreover, surfactants may play an important role in the digestion of proteins by denaturing the substrate, and thus, exposing more sites for proteolytic activity (Mole and Waterman, 1985).

Since the interfering action of surfactants in the precipitation of proteins by tannins may be due to surfactant–tannin precipitation (DeVeau and Schultz, 1992), high contents of tannins in the ingested food may even in species with high concentrations of surfactants, cause nutritional deficiencies.

The effects of hydrolyzable and condensed tannins on consumption, digestion and assimilation of food in phytophagous insects have been examined in detail (reviewed in Bernays, 1981; Mole and Waterman, 1987; Hagerman and Butler, 1991), It has been established that they act as toxins and as feeding inhibitors (e.g. Bernays, 1981; Karowe, 1989). In contrast to phytophagous insects, little is known about the influence of phenolic compounds in the litter on saprophagous soil animals. Generally, phenolics are thought to impair decomposition processes (Harrison, 1971; Savoie and Gourbière, 1989). Although many phenolics are readily removed from the litter by leaching (Kuiters and Sarink, 1986), the effects of tannins on the reproduction and mortality of terrestrial isopods (Isopoda: Oniscidea) have been demonstrated recently (Zimmer and Topp, 1997). Since the gut fluids of terrestrial isopods are slightly acidic (Hartenstein, 1964; Zimmer and Topp, in press), gut fluid detergency may play an important role in interfering with the precipitation of ingested plant protein.

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The present study was performed to investigate surfactants in the gut of the saprophagous isopod, *Porcellio scaber*, and their interactions with ingested phenolics.

MATERIAL AND METHODS

Individuals of *Porcellio scaber* (Isopoda: Oniscidea) were collected in a poplar forest near Cologne (Germany). In the laboratory, the woodlice were kept separately in small Petri dishes, the bottoms of which were covered with Plaster of Paris to maintain sufficient humidity. Prior to the experiments, specimens were fed with litter originating from the forest where the isopods had been collected. Only adult isopods were taken for experiments. Each measurement was conducted with 10 specimens.

For the determination of the surface tension of the gut fluids, the hindguts were dissected, and the contents pushed out of the gut cuticle after removing the surrounding tissue. The gut contents were extracted individually for 10 min in 10 μl of a mixed buffer solution with the following composition: 3 mM NaCl, 227 mM KCl, 300 mM fructose, 175 mM NaH_2PO_4, 25 mM Na_2HPO_4 (Giordana and Sacchi, 1978). The pH value of the buffer solution (pH 6.1) was chosen to be comparable to the pH level of the hindgut (Hartenstein, 1964; Zimmer and Topp, in press). The extracts were centrifuged for 5 min at 25,500 g. To measure surface tension, as little as 5 μl of the solution was introduced into a capillary (r = 0.5 mm) using the apparatus described by Ferguson (1943).

Surface tension of the fluids was calculated as $\gamma(\mathrm{N/m^2})\frac{(hrdg)}{2}$, with

h = measured value (m)

r = radius of the capillary (0.000,5 m)

d = density of the measured fluid (= 1)

g = gravity (9.81 m s^{-2}).

In order to estimate the 'critical micelle concentration' (CMC), the concentration at which there is a transition between the surfactant in the free unassociated state and the micellar state (Martin *et al*., 1987), the surface tension of a series of dilutions of the initial extract of the gut content was measured. The CMC was identified as an abrupt increase in surface tension (cf. Martin and Martin, 1984).

An estimation of the effect of ingested phenolics and the pH of the litter was performed by feeding the isopods food sources that varied in pH and phenol content (Table 1). Since leaching plays an important role in removing phenolics from leaf litter (Kuiters and Sarink, 1986), the phenol content of the food sources was described in terms of the leaves' 'state of leaching' (Table 1).

In addition to the original litter (pH 6.5–7.0; 'completely leached'), isopods were fed birch litter (*Betula pendula*) that had been collected immediately after leaf fall. This 'unleached litter' (pH 5.0 ± 0.3) served as a control for other treatments. Leaching was simulated by soaking the litter in aqueous solutions of sulphurous acid at pH 2.0 and 5.0 for seven days (Zimmer and Topp, 1997), resulting in pH levels of the leaves (3 M KCl) of 2.7 ± 0.4 and 4.5 ± 0.3, respectively. These treatments also produced litter with different phenol levels (Zimmer and Topp, 1997) and thus, were described as 'poorly leached' (pH 2.7) and 'leached' (pH 4.5). Further variation in leaf litter was obtained by enriching the litter with phenolic compounds. Air-dried birch leaves were soaked in stirred solutions of tannic acid (10%) or gallic acid (5%), respectively, for three days.

In order to obtain information on the effect of the treatments described above, the total content of phenolics was determined as described in Julkunen-Tiitto (1985) and the content of gallotannins was measured after Inoue and Hagerman (1988). These methods were modified for small samples by reducing the volumes. 50 mg (dw) of randomly selected leaf aliquots were extracted twice in 1 ml of 50% methanol at 60°C for 3 h. After centrifuging the extracts (5 min at 25,500 g), the supernatant solution was used for the phenol determination. 100 μl of the extract was diluted with 700 μl of double-distilled water. Subsequently, 200 μl of Folin–Ciocalteu reagent (Merck, Darmstadt, Germany) was added, and the mixture was shaken vigorously. Twenty min after adding 1000 µl of a 20% Na_2Co_3 solution, the absorbance at 700nm was measured. Phenol (Sigma, St. Louis, MO, USA) served as a standard. For the determination of gallotannins, 100 μl of the methanolic extract was mixed with 75 μl of 0.667% methanolic rhodanine. After 5 min, 50 μl of 0.5 M of KOH was added. After adding 975 μl of double-distilled water, the absorbance at 520 mn was determined. Gallic acid (Sigma, St, Louis, MO, USA) served as a standard. Chemical analyses were conducted with 10 replicates each.

Since most of the obtained data on surface tension of gut fluids, and phenolic compounds of the litter were not normally distributed, the results are described as median ± median absolute deviation (M ± MAD). Comparison of different samples were performed using the Kruskal–Wallis H test. Subsequently, significant differences were localized with Mann–Whitney U tests. The multivariate set of data on pH levels and content of gallotannins and total phenols was analyzed with a three-way ANOVA after transforming the data to normality [$x' = \log(x + 1)$]. In this way, information on the effect of the measured leaf characteristics on the surface tension in the gut of *P. scaber* after feeding on the different food sources were obtained.

RESULTS

Gut fluids of *Porcellio scaber* fed on litter taken from the field were characterized by a surface tension of (3.9

TABLE 1. Experimental design with untreated and manipulated food sources

	'Completely leached' (ORIG)	'Leached' (be50)	'Poorly leached' (be20)	'Unleached' (be-c)	Gallic acid-enriched (+ GA)	Tannic acid-enriched (+ TA)
pH	6.7 ± 0.3	4.5 ± 0.3	2.7 ± 0.4	5.0 ± 0.3	4.9 ± 0.2	5.0 ± 0.2
Phenolics	Low	Medium	High	High	High	Very high
Gallotannins	Very low	Low	Low	Low	Medium	High

TABLE 2. Three-way ANOVA to estimate the effects of pH levels and phenolics of the leaves on surface tension in *Porcellio scaber*

Three-way ANOVA	*SS*	*DF*	*MS*	*F*	r^2	*p*
Total phenolics	232.39	3	77.46	6.40	0.22	0.002
Gallotannins	126.25	2	63.13	5.21	0.12	0.013
pH level	5.40	1	5.40	0.45	0.01	0.511
Model	755.54	5	151.11	12.48	0.72	0.000
total	1046.12	29				

± 0.3) 10^{-5} J m^{-2} (Fig. 1a). This value was significantly lower ($p < 0.001$) than that of the buffer used for extraction (7.0×10^{-5} J m^{-2}).

The dietary history of *P. scaber* strongly influenced the surface tension of the gut contents (Fig. 1a). Surface tension significantly increased, depending on the total content of phenolics (Fig. 1b) or gallotannins (Fig. 1c). To evaluate the effects of these leaf characteristics on the surface tension of the gut fluids, a three-way ANOVA with the pH level, the phenol content, and the gallotannin content of the leaves as 'sources of variation' was performed (Table 2). 72% of the variance in surface tension could be explained statistically ($r^2 = 0.72$; Table 2). The total content of phenolics explained 22% of variance ($p = 0.002$). An additional 12% were explained by the content of gallotannins ($p = 0.013$), while the pH levels of the litter did not show any significant effect.

About 1.0 ± 0.3 μl of fluids were present in the gut lumen of adult isopods. Hence, extracting in 10 μl buffer solution means an 8–12-fold dilution. Taking this into account, the observed effect of further dilution of the extract (Fig. 2) suggests that surfactants in the gut of *P. scaber* are present at concentrations at least 80-fold greater than the CMC.

DISCUSSION

Tannins mainly tend to adversely affect species which do not normally feed on plants containing much phenolics (Bernays, 1981). Many kinds of phenolics are removed from leaf litter by leaching (Kuiters and Sarink, 1986). According to Bernays (1981), isopods that feed on food low in phenolics can be expected to be sensitive to tannins. However, surfactants that effectively reduce the impact of ingested phenolics in insect guts (Martin and Martin, 1984; Martin *et al.*, 1985) are present in the gut fluids of *P. scaber*. The surface tension of the gut fluids in *P. scaber* agrees well with data presented for phytophagous insects (33–42 dynes cm^{-1} = 3.3–4.2 × 10^{-5} J m^{-2} in larvae of *Manduca sexta* (Lepidoptera). Martin and Martin, 1984; 3.7 × 10^{-5} J m^{-2} in *Schistocerca gregaria* (Orthoptera); (Martin *et al.*, 1987). DeVeau and Schultz (1992) reported a surface tension of 3.2 × 10^{-5} J m^{-2} in the gut fluids of gypsy moth larvae (*Lymantria dispar*, Lepidoptera) feeding on artificial diet. In *M. sexta* larvae, surface tension of the gut fluids was not affected by feeding on artificial diet (Martin *et al.*, 1987). In *P. scaber*, feeding on lipid-free artificial diet (cf. Carefoot, 1984) led to a higher surface tension (64–69 × 10^{-5} J m^{-2}, data not illustrated) similar to that of the buffer solution (69–73 × 10^{-5} J m^{-2}) Normally, surfactants arise in the gut from hydrolysis of ingested lipids (Turunen, 1983). Thus, surface tension of an animal's gut fluids depends on its dietary history (Martin *et al.*, 1987). However, DeVeau and Schultz (1992) suggested that gypsy moth larvae are able to 'recharge' lost gut surfactants.

The observed effects of ingested phenolics on surface tension (Table 2) suggest that surfactants in the gut fluids of *P. scaber* exhibit properties similar to those in phytophagous insects in binding to phenolics, and by this, reducing the potential impact of ingested tannins (cf. DeVeau and Schultz, 1992). Consequently, large amounts of ingested tannins reduce the concentration of free surfactants, and thus, cause increased surface tension of the gut fluids. Within the broadly defined groups of phenolics, the class of gallotannins may be of particular interest (Table 2). Gallic acid, an important hydrolysis product of gallotannins, had a significant effect on the surface tension. The treatments with enriched gallic acid (+ GA) and enriched tannic acid (+ TA) differed significantly concerning their contents of gallotannins ($p < 0.01$; Fig. 1c), but did not show different effects on the

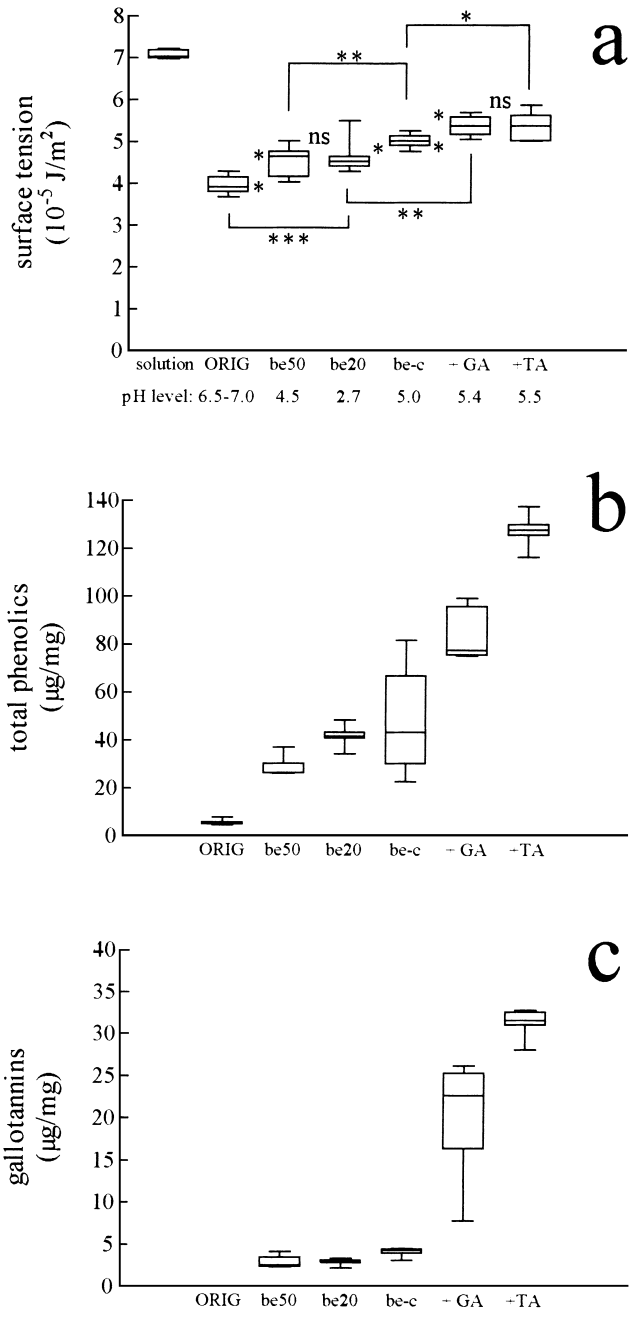

FIGURE 1. Surface tension of gut fluids of *Porcellio scaber* (a) feeding on various food sources, differing concerning the total content of phenolics (b) and the content of gallotannins (c). Data in box-plots are presented as minimum, median, first and third quartiles, and maximum (n = 10, each). solution: buffer solution (pH 6.1); ORIG: overwintered poplar litter originating from the field, be50: freshly fallen birch litter. leached at pH 5.0; be20: freshly fallen birch litter, leached at pH 2.0; be-c: freshly fallen birch litter, untreated control; + GA: freshly fallen birch litter, enriched with gallic acid; + TA: freshly fallen birch litter, enriched with tannic acid. Asterisks mark significant differences between samples (U test): *: $p < 0{,}05$; **: $p < 0.01$; ***: $p < 0.001$; ns = not significant.

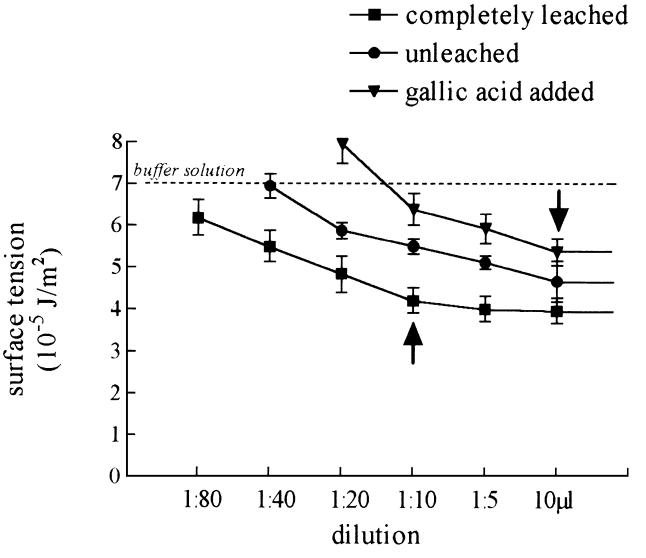

FIGURE 2. Effect of dilution on the surface tension of gut fluids of *Porcellio scaber* feeding on various food sources: poplar litter originating from the field ('completely leached'), freshly fallen birch litter, leached at pH 2.0 ('poorly leached'), and freshly fallen birch litter, enriched with gallic acid ('gallic acid added'). Data are presented as median ± median absolute deviation (n = 10, each). Arrows mark the dilution at which an abrupt increase of surface tension was observed.

surface tension ($p > 0.8$; Fig. 1a). DeVeau and Schultz (1992) also observed that adding tannic acid to midgut fluids of *L. dispar* elevated the surface tension.

Tannic acid and red oak tannin precipitated the gut surfactants of *L. dispar*, leading to a reduction of surface active phospholipids (DeVeau and Schultz, 1992). Consequently, tannins may cause lipid deficiencies in phytophagous insects in addition to reducing the digestibility of ingested food or precipitating digestive enzymes by protein-complexing (DeVeau and Schultz, 1992). Furthermore, tannins might also bind to lipids in the epithelial cell membranes (DeVeau and Schultz, 1992) if they permeate through the membranes surrounding the food bolus ('peritrophic envelope') and reach the epithelium (cf. Barbehenn and Martin, 1992, 1994).

As indicated, surfactants are present in the gut of *P. scaber* at concentrations at least 80-fold greater than the CMC (Fig. 2). In *L. dispar* larvae, the surfactant concentration was 8-times CMC, which was determined to be about 80 μM (DeVeau and Schultz, 1992). Similar values were observed in *M. sexta* and *S. gregaria* (Martin and Martin, 1984; Martin *et al.*, 1987). In *P. scaber*, the effect of dilution on the surface tension of gut fluids varied with the dietary history (Fig. 2). In comparison to the 'completely leached' control from the field and the 'unleached' samples of freshly fallen birch leaves, the gallic acid-enriched treatment was chosen as an example to elucidate the effects of certain phenolics on surfactants in the gut fluids of *P. scaber*. As illustrated in Fig. 2, the concentration of free surfactants was about 10-fold higher in isopods feeding on 'completely leached' leaves than in those that fed on litter with higher contents of phenolics (cf. Fig. 1b, c).

Mainly the products of phenol oxidation are thought to precipitate proteins (Appel, 1993). Presumably, surfactants in the gut fluids of *P. scaber* reduce the impact of ingested phenolics or their oxidation products (cf. Martin and Martin, 1984; Martin *et al.*, 1985). Moreover, surfac-

tants inhibit polyphenoloxidase activity (Felton and Duffey, 1991). However, enzymatic oxidation of phenolic compounds by peroxidases or polyphenoloxidases is required for their biodegradation by microorganisms (e.g. Ander and Eriksson, 1976; Sinsabaugh and Linkins, 1987; Thurston, 1994), and this may be very important with respect to the digestion of lignocellulose by saprophagous animals (Reid, 1983; Ljungdahl and Eriksson, 1985; Sinsabaugh and Linkins, 1987; Breznak and Brune, 1994), and during decomposition (cf. Hartenstein, 1982).

Many polyphenoloxidases show maximal activity at about pH 5–7 (Mayer and Harel, 1979; Wood, 1980). Similar pH optima have been described for cellulases (Hartenstein, 1964; Zimmer and Topp, in press) and other digestive enzymes in the gut of terrestrial isopods (e.g. Alikhan, 1968; Clifford and Witkus, 1971; Beck and Friebe, 1981). Thus, although an acidic pH level in the gut increases the risk of being adversely affected by ingested tannins, (Berenbaum, 1980; Martin and Martin, 1983; Schultz and Lechowicz, 1986), the acidic pH level of about 6 in the gut of *P. scaber* (Hartenstein, 1964; Zimmer and Topp, in press) appears to be a physiological adaptation to optimize enzymatic activity with respect to digestive processes (Zimmer and Topp, in press). Harmful effects of ingested phenolics are prevented by high concentrations of surfactants in the gut fluids.

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