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Selective consumption and digestion of litter microbes by *Porcellio scaber* (Isopoda: Oniscidea)

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Dedicated to Werner Topp, Köln, to mark his retirement and to express gratitude for having had the opportunity to conduct research under his supervision.

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Actinomycetes;
Feeding preference;
Isopoda;
Leaf litter-colonising microbes;
Nutritive value

Summary

In feeding preference tests with artificial diets consisting of food sources inoculated with different types of litter microbes, *Porcellio scaber* was capable of discriminating between different microbe species. Generally, microbial colonisation increased the attractiveness of a given food source, in particular, when the food source was of low quality (cellulose) and when food sources were inoculated with single species of actinomycetes (*Streptomyces celluloflavus* or *Pseudonocardia autotrophica*). In most cases, actinomycetes (Gram-positive bacteria) were preferred over both Gram-negative bacteria and fungi, whether or not these microbes exhibited cellulolytic activity. Enzymatic *in vitro* digestion of both the Gram-positive *S. celluloflavus* and *P. autotrophica* was significantly greater than that of Gram-negative bacteria (*Pseudomonas fluorescens* and *Myxococcus xanthus*) or fungi (*Chaetomium globosum* and *Fusarium ventricosum*). *S. celluloflavus* biomass was more effectively incorporated into isopod biomass than that of fungi and Gram-negative bacteria; *P. autotrophica* was more effectively incorporated into isopod biomass than that of Gram-negative bacteria. Based on these results, we hypothesise that *P. scaber* preferentially feeds on those microbes that it can readily digest. Whether this holds true for other Gram-positive bacteria or for other detritivores awaits investigation.

Introduction

Both free-living and symbiotic microbes play a crucial role in the nutrition of soil invertebrates that feed upon nitrogen-poor food sources. Terrestrial isopods, for instance, that feed on

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nitrogen-poor leaf litter and woody debris depend upon detritus-colonising microbes that they ingest along with the food (summarised in Zimmer 2002). Three possible reasons for this particular animal–microbe interaction have been proposed and debated during the last few decades (for discussion, see Kautz et al. 2002; Zimmer et al. 2003):

(1) Microbial processing of detritus, both prior to feeding and during the gut passage, facilitates its digestive utilisation (Rushton and Hassall 1983; Kukor and Martin 1986; Hassall et al. 1987; Zimmer 1999).
(2) Microbial biomass is digested and utilised as source of nutrients (Reyes and Tiedje 1976; Coughtrey et al. 1980; Márialigeti et al. 1984; Gunnarsson and Tunlid 1986; Hassall et al. 1987; Zimmer and Topp 1998).
(3) Ingested microbes help maintain gut conditions that are favourable for digestive processes (Zimmer 1997; Zimmer and Topp 1997).

In either case, selective feeding by detritivores on particular types or even species of microbes with specific characteristics would be expected (e.g., Hedlund and Öhrn 2000: Collembola; De Mesel et al. 2004: Nematoda) in order to maximise nutritive gain from feeding on microbially colonised detritus, since different microbes probably exhibit different digestibilities and nutritive values (for discussion, see Scheu and Folger 2004). Selective feeding activities are of ecological significance because of the resulting shifts in physiological characteristics and capabilities of microbial communities that consequently affect the efficiency of decomposition processes (cf. Sinsabaugh et al. 2002). However, except for an early study by Gunnarsson (1987), no such discriminative capability has been described for macrofaunal detritivores, nor has a relationship between feeding preference for, and digestibility of, particular microbes been demonstrated in soil detritivores.

The aim of the present study was to evaluate the effects of different microbes on feeding activities of *Porcellio scaber* on low- versus high-quality food sources. Specifically, with respect to the above hypothesis (2), we predicted both differential digestive breakdown and utilisation (in terms of biomass production) of microbes, possibly owing to different cell wall compositions of fungi and Gram-negative or -positive bacteria. Further, we expected that those species that can be converted into biomass more efficiently are preferred over others. We hypothesised more pronounced selective feeding to occur on low-quality food sources, since microbial biomass, as a supplementary source of nutrients (cf. Zimmer et al. 2003), should be more important if the basal food source is hard to digest. According to the above hypothesis (1), we expected that cellulolytic microbes would be preferred over non-cellulolytic ones, at least when the isopods were offered a cellulose-rich, low-quality food source.

Material and methods

Isopods

P. scaber Latreille, 1804 individuals were collected in oak woodlands in the vicinity of Kiel, Germany. In the laboratory, isopods were maintained in groups of 10–20 randomly chosen individuals in translucent plastic containers ($18 \times 11\,cm^2$), the bottoms of which were covered with soil and leaf litter from the collecting sites, at 15 °C, 16 h L (light):8 h D (dark).

Microorganisms

Oak (*Quercus robur*) leaf litter from the collecting sites was used to extract and cultivate naturally occurring microorganisms that were utilised in the first set of feeding preference tests. Litter was manually cut in small pieces (ca. $0.5\,cm^2$) and thoroughly mixed. Aliquots of 2 g of this mix derived from different leaves, together with 10 sterile glass beads (6 mm), were added to 100 mL autoclaved tap water. After shaking for 15 min (420 rpm) on a horizontal shaker and sedimentation for 5 min, 1 mL of the supernatant was diluted 1:10 four times with sterile tap water. Aliquots of 100 µL of each dilution step were spread on three different agar plates, each. Agar plates were prepared for culturing fungi, all bacteria, and actinomycete bacteria. Agar for the selective cultivation of fungi (after Parkinson 1994) contained the bactericidal antibiotic streptomycin, and both agar for all bacteria (after Zuberer 1994) and agar for the cultivation of actinomycetes (after Wellington and Toth 1994) contained the fungicide cycloheximide.

For the second set of feeding preference tests, we used single species cultures of fungi and bacteria that are commonly found in soil and leaf litter, namely the fungi *Chaetomium globosum* (cellulolytic) and *Fusarium ventricosum*, the Gram-negative bacteria *Pseudomonas fluorescens* (cellulolytic) and *Myxococcus xanthus*, and the Gram-positive actinomycetes *Streptomyces celluloflavus* (cellulolytic) and *Pseudonocardia autotrophica*; all cultures were