



Original article

Mucilaginous seeds and algal diets attract soil Collembola in preference tests



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ABSTRACT

Collembola are abundant in soils and with primary producers interact directly (by grazing algae, seeds, seedlings or roots) or indirectly (by altering the composition of soil microbial communities). Direct collembolan herbivory influences the establishment of seedlings and the dynamics of plant populations whereas grazing on algae affects their biomass, community composition and dispersal. Studies on feeding behaviour of Collembola have mainly focused on fungi, whereas primary producers as resources have seldom been studied. We assessed the feeding preference of two Collembola species (*Folsomia candida* and *Folsomia fimetaria*) for food sources from different functional groups using dual choice olfactometers. A preferred fungal species (*Alternaria alternata*) was compared with two terrestrial microalgae (*Chloroidium angusto-ellipsoideum* and *Pabia signiensis*) as well as mucilaginous seeds (*Plantago major*). A second experiment investigated the choice behaviour of *F. candida* between different species of common green algae in soils (*Chlorella vulgaris*, *Stichococcus mirabilis*, *Stichococcus bacillaris* and *Coccomyxa* sp.). Generally, feeding preferences stabilised over 48 h. *F. candida* avoided *P. signiensis* compared to the other three food sources whereas *F. fimetaria* preferred the seeds of *P. major* to the alternative diets. When only soil algae were offered, *F. candida* was able to distinguish between different species: *S. mirabilis* was clearly preferred to *S. bacillaris* and *C. vulgaris*. Our results reflect that both Collembola may use a wide range of resources if available and differ in their preference behaviour. Selective feeding on algae or mucilaginous seeds has the potential to modify soil microorganism communities, soil properties and the establishment of seedlings.

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1. Introduction

Microarthropods, mainly consisting of Collembola and mites, are the dominant arthropods in the majority of soils. Feeding predominantly on soil fungi and bacteria, they affect their activity and community composition and associated nutrient mineralisation [1,17,49]. For a long time this indirect effect on nutrition availability has been regarded the main interaction route between microarthropods and primary producers, beside occasional reports of herbivory [61,62]. Around the turn of the millennium it was realised that plant-Collembola interactions could be shaped by tri-trophic interactions [52,65]. Several studies investigated the effects of Collembola in these, up to plant associated herbivores such as phloem feeding aphids [20,29,54]. The impact of Collembola could

range from negative through neutral to positive, depending on plant species [54,67]. Recently, it has been documented that Collembola as root herbivores [16] induce the expression of defence-related genes in the model plant *Arabidopsis thaliana* [15]. Other studies on plant-mediated links between soil fauna and above-ground herbivores, interactions between plant roots, exudates, Collembola and microbes and their influence on plants growth and community assembly have received considerable attention [4,13,14,42,55]. Moreover, Rosenstiel et al. [48] demonstrated the potential pollination mutualism between springtails and mosses mediated via chemical cues similar to some plant-pollinator systems. Furthermore, Collembola are also known to influence seed germination rates and thus plant productivity [38,39]. The effects of Collembola on seed germination could be positive by suppression of fungal seed pathogens [38,39] or negative by direct grazing [43]. Nietschke et al. [43] gave evidence that *Folsomia candida* fed on the mucilaginous seed coat as well as on the seed embryo of *Plantago major* and suggested a direct influence on seedling emergence. However, the manifold direct and indirect interaction pathways

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between Collembola and primary producers are still poorly understood.

Many studies have focused on Collembola–fungi interactions [45,55,60] as major functional groups in soil decomposition processes [1,23]. A wide range of fungal taxa have been investigated in laboratory food choice experiments and demonstrated Collembola to strongly select between fungi [26,32,40,56]. It has been proven that Collembola use fungal odours to discriminate between them [2,22,58] and show a clear preference for dark pigmented fungi (e.g. *Alternaria*, *Cladosporium*) which contain more carbon and nutrients and are less toxic than other fungi [30,31,36]. These saprophytic fungi are often involved in the decay of seeds [51]. Less prominent food sources like algae, bacteria or plant tissue have been largely neglected in such studies, although it is known that bacteria, algae or soil animals such as nematodes are also accepted or even preferred to fungi [21,35,64].

For many surface-living Collembola species green algae are an important food source [10,63,64], and even euedaphic species thrive well when feeding on unicellular terrestrial algae [7]. Using nitrogen stable isotope analysis, Chahartaghi et al. [9] investigated 20 Collembola taxa from three deciduous forest stands; potential food sources included algae, mosses, lichens and other plant-derived materials. They ranked Collembola into three different feeding guilds. The phycophagous/herbivorous guild contained exclusively surface living species, yet isotope signatures indicated that also the hemiedaphic species *Folsomia quadrioculata* may switch to this type of diet. Even though the importance of algae for Collembola has long been recognised, only few studies included green algae when testing food selection [18,64]. Verhoef et al. [64] showed that *Tomocerus minor* consumed algae at higher rates than fungi in feeding preference tests, with positive influence on body growth. In turn, *Orchesella cincta* thrived better on fungi [64]. Buse et al. [7] measured higher body mass in three Collembola species after consumption of the green algae *Chlorella vulgaris* compared to filamentous green algae and cyanobacteria and suggested that *C. vulgaris* could be a high-quality food resource. Studies from Davidson and Broady [12] and Buse et al. [8] revealed that Collembola are also dispersal vectors for green algae, which emphasises the importance of interactions between these two groups. If Collembola are also able to differentiate between algal cues (originating from different species), selective feeding and an associated impact on the composition of algal communities is quite possible. Preferential feeding on different species of green algae has been proven for mites [24], yet for Collembola this has never been investigated.

Thus far most collembolan food preference studies have focused solely on one functional group and thus lack diet diversity. We examined collembolan food choice involving three different functional groups, a saprophytic soil fungus, six species of terrestrial green algae and seeds of *P. major*. Additionally, we examined species-specific differences in preference, testing the food choice of two euedaphic Collembola species, *F. candida* and *Folsomia fimetaria*. The questions we asked were: (1) Is preferential feeding of Collembola detectable between food types from different functional groups (fungi, seeds and algae)? (2) Are dark-pigmented fungi preferred over algae? (3) Are there any differences in preference between the two Collembola species studied? (4) Do Collembola select between different species of soil algae?

2. Materials and methods

2.1. Collembola

Individuals of *F. candida* (Willem) originated from our established laboratory culture. Specimens of *F. fimetaria* (Linnaeus) were

obtained from Z. Gavor, Department of Terrestrial Ecology at the National Environmental Research Institute in Silkeborg, Denmark. Both species were reared in plastic vessels (Ø 7.5 cm, height 3 cm) containing a bottom layer of plaster of Paris/charcoal mixture (9:1). Cultures were stored at 20 ± 1 °C in the dark and kept moist with distilled water. Synchronised individuals were fed with dried baker's yeast. Only adult animals (28 days old) were used in the study. Individuals of *F. fimetaria* were not differentiated between male and female. Collembola used in the study were starved for 48 h before introducing them into the experimental system.

2.2. Diet organisms

Eight diet organisms were offered as food choice: (1) the dark-pigmented microfungus (Dematiaceae) *Alternaria alternata*; (2) the ellipsoidal green algae *Chloroidium angusto-ellipsoidea* (Hanagata and Chihara; Darienko et al., syn. *Chlorella angustoellipsoidea*); (3) the coccal green algae *C. vulgaris* (Beijernick); (4) the spherical to ellipsoidal green algae *Pabia signiensis* (Friedl and O'Kelly); (5) the rod-shaped green algae *Stichococcus mirabilis* (Lagerheim); (6) the rod-shaped green algae *Stichococcus bacillaris* (Nägeli); (7) the spherical to ellipsoidal green algae *Coccomyxa* sp.; (8) moistened seeds of *Plantago major* L. (Plantaginaceae).

2.2.1. Fungus

The fungal strain *A. alternata* originated from our laboratory culture sample and was cultivated on 2% malt agar (20 g agar L^{-1} , $20 \text{ g malt extract L}^{-1}$, $10 \text{ mg Novobiocin L}^{-1}$). Cultures were stored at room temperature in the dark. After 2–3 weeks, depending on growth rate, a disc of fungal mycelium (Ø 1 cm) was cut out of the external hyphae and was transferred into the respective choice chamber (Fig. 1).

2.2.2. Algae

All strains of green algae were obtained from the Culture Collection of Algae at Göttingen University, Germany (SAG). These microalgae were originally isolated from terrestrial habitats and most of them are abundant in different kind of soils [6,11,25,47]. For the experiments, the algae species were grown on agar plates with Bold's Basal Medium (BBM) [3,59]. Samples were kept at room temperature with a light–dark cycle of 12:12 h (1500 lx at the surface of the Petri dish lid). After two weeks samples were harvested using a sterilised scoop. A piece of cell colonies with a



Fig. 1. Dual choice olfactometer design. Three plastic vessels (Ø 5 cm, height 3 cm, filled with Plaster of Paris layer) were connected via two silicon tubes. For eased passage from the starting chamber (indicated with a red dot) into the choice chamber, moist filter paper was laid though the tubes. Choice chambers were provided according to experiment 1 and 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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