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Barley straw decomposition with varied levels of microbial grazing by *Folsomia fimetaria* (L.) (Collembola, Isotomidae)

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Summary. *Folsomia fimetaria* (L.) were added (0, 5, 10, 20 animals) to 0.100 g barley straw which had been inoculated 10 days (244 h) earlier with a natural soil microflora. Respiration (CO_2 evolution) was monitored continuously. Mass loss, fungal standing crop (total and FDA-active), bacterial and protozoan biomass were estimated 42 days (1,000 h) after microbial inoculation. The degree of surface cover by hyphae was surveyed at regular intervals. No significant differences ($P > 0.05$) were found in respiration, mass loss or microbial biomass, but the density of surface hyphae were reduced by addition of Collembola. Fungal production was low, less than 5% of the estimated microbial production, and could not account for all collembolan growth during incubation. *F. fimetaria* appeared to consume mainly bacteria and protozoa, and had little impact on carbon mineralization.

In most ecosystems soil animal communities are directly responsible for a small fraction of the total C mineralized (Anderson et al. 1981; Petersen and Luxton 1982). Only a minor part of this fraction comes from collembolan respiration, suggesting that Collembola contribute very little to decomposition. However, soil microarthropods may consume a substantial part of net fungal production (Persson et al. 1980) and may influence C mineralization and nutrient cycling to a greater extent than is indicated by their contributions to total respiration (Macfadyen 1963; Hanlon and Anderson 1979; Petersen and Luxton 1982; Persson 1983).

In recent reviews (Anderson et al. 1981; Petersen and Luxton 1982; Parkinson 1983; Anderson and Ineson 1984) several examples of inhibition and stimulation by mesofauna are discussed. Effects are often found in simple systems, containing only one or two fungal species and a grazer (Hanlon and Anderson 1979; Parkinson et al. 1979; Hanlon 1981a; Bengtsson and Rundgren 1983) where negative effects can be attributed to consumption of hyphae and positive effects can be attributed to dispersal of microbial propagules by the animals or introduction of other microorganisms with the added animals (Visser et al. 1981). However, in more complex laboratory systems the effects on decomposition are often insignificant or inconclusive (Addison and Parkinson 1978; Bååth et al. 1981; Hassall et al. 1983).

Field studies of microarthropods, including litter-bag techniques (Andrén and Lagerlöf 1983), indicated that *Folsomia fimetaria* were abundant in decomposing barley straw and thus may have been important in straw decomposition processes. *F. fimetaria,* an isotomid collembolan, is an unpigmented, soil-dwelling species with an adult body length between 0.8 and 1.4 mm (Gisin 1960). A laboratory experiment was performed to test the hypothesis that *F. fimetaria* influenced the decomposition rate and microbial biomass of barley straw in the early stages of decomposition.

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Material and methods

Respiration was measured in air-tight containers using the headspace method (Fig. 1). The containers were made from perspex tubes with an inner diameter of 36 mm and a height of 60 mm (Rosswall et al. 1977). The lids, sealed with a rubber O-ring, had two rubber septa, one for aeration needles and one for the sampling syringe. The containers were aerated with moist air between gas samplings by passing the incoming air through partly water-filled test tubes. Air bubbles passing through the test tubes served as a simple flow meter which was used to maintain a similar air flow through all containers.

A 20 mm high sample holder, made of plastic tubing, was placed inside each container. A terylene net, on which

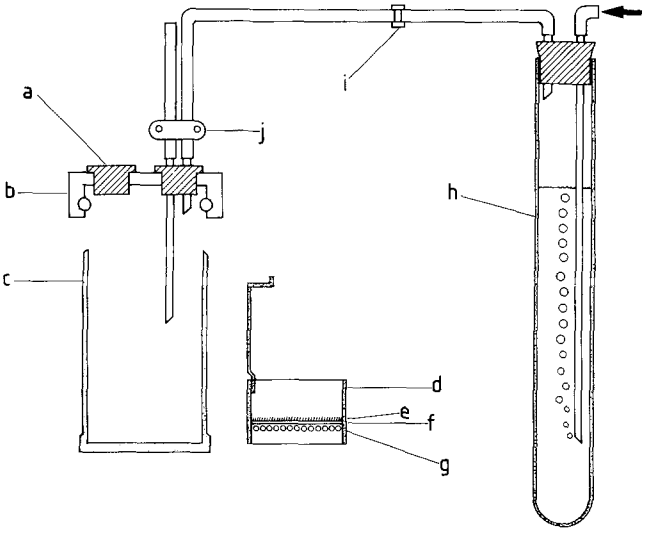

Fig. 1. The air-tight container. Rubber septum (*a*), lid with O-ring (*b*), air-tight container (*c*), substrate holder (*d*), straw substrate (*e*), glass fibre filter (*f*), terylene net (*g*), test tube with water (*h*), valve for aeration control (*i*), shutoff valve for incubation (*j*)

rested a glass fibre filter, was glued to the bottom of the sample holder. The substrate, 0.100 g ground barley straw, sieved through 1 mm mesh, was evenly distributed on the glass fibre filter and then rinsed with 50 ml of tap water sucked through the filter by a water pump. The sample holders with the straw were dried at 40° C, and 5 ml filtered soil suspension (1 g moist soil in 2 l tap water) was added. The sample holders with the straw were dried at 40° C for 24 h and weighed to within an accuracy of 0.1 mg. The samples were then remoistened on a suction flask, to a water content of around 70% of the wet mass, placed in the air-tight containers and kept at 15° C throughout the 42 day (1,000 h) experiment. Mean ash-free dry mass of the straw substrate before incubation was 88.0 mg (S.E. = 0.3 mg, $n=28$). Chemical analyses were made according to Berg and Staaf (1980), and the nitrogen content was 1.0%, carbon 44%, Klason lignin 15.6% and water solubles 5.7%. The headspace in the containers was sampled every 24 h, and then aerated for 3 h before closure. Towards the end of the experiment the closure time was increased to 72 h, to obtain sufficient concentrations of CO_2 for accurate analyses. The concentrations of CO_2 in the containers were normally around 0.5% at sampling and were never allowed to exceed 1%. Evacuated blood sampling tubes (Venoject T-273, Terumo Corp., Tokyo, Japan) were used for gas samplings and calibrations, by needle extraction of 3.0 ml gas. A 1.00 ml subsample was injected into a Perkin-Elmer Model 3920 Gas Chromatograph with a 2 m column packed with Porapak QS and run at 100° C. A Perkin-Elmer thermal conductivity detector (TCD) connected to a Perkin-Elmer M-2 Calculating Integrator gave integrated peak area values.

Collembolan respiration was calculated for each sampling occasion (see below) and subtracted from total respiration to give microbial respiration. The amount of surface hyphae was estimated at 15× magnification using a stereo microscope. A scale ranging from zero to ten was used, with zero representing no visible hyphae and ten representing total cover. The estimates were performed as a blind test, without a key to the treatments.

Collembola were taken from a laboratory culture, kept at 15° C on plaster of Paris and charcoal mixture according to Hutson (1978), with barley straw as substrate. After the containers with straw had been incubated 244 h, the animals were transferred to the containers by means of an exhaustor. Five, ten or 20 animals were added to seven replicates each. These numbers were chosen to obtain abundances similar to, and higher than those in straw litter-bags incubated in the field by Andrén and Lagerlöf (1983). A control series with seven containers received no animals. The containers were examined every three days for dead animals, which were removed and replaced. To avoid reproduction during the experiment, juvenile animals were used (0.75 mm body length, 2.3 µg dry mass, weighed on a Cahn 4700 Automatic Electrobalance). A multiplication factor of 3.33 was used to obtain fresh mass, according to Persson et al. (1980).

The individual fresh mass (M µg) increase was fitted to an exponential equation ($M_{(t)}=M_{(0)}\cdot e^{kt}$, $k=0.001878\ h^{-1}$), and the mass at every gas sampling occasion was calculated. Using parameters for Collembola from Persson et al. (1980), individual respiration (O_2 consumption) was calculated for each gas sampling occasion. A RQ of 0.8 was used to convert O_2 consumption to CO_2 production, which was converted to µg carbon using the general gas law. The results were multiplied by the number of animals present and the integrated animal respiration was calculated. The total respiration measured was also integrated, and total microbial respiration was calculated as the difference. For every sampling occasion an analysis of variance (factor: animal number) was made for total measured and microbial respiration. The experiment was terminated after 42 days (1,000 h), when juveniles started to hatch.

After the incubation three replicates from each treatment were turned upside down over small plastic cups and heated by an overhead lamp to extract the animals. Five animals were freeze-dried and weighed. The straw and filters were then dried at 40° C and weighed to obtain substrate mass loss during the incubation.

Total fungal length was estimated on the dried straw which was scraped off the glass fibre filter, weighed and homogenized in 10 ml water for 5 min using a Turrax ultramixer at 25,000 rpm. The homogenate was diluted 40 times with water. One ml of the diluted homogenate was filtered onto a 0.8 µm membrane filter (Millipore) and stained with Loeffler's methylene blue. The filters were inspected in a phase contrast microscope at 400× magnification. In every filter 50 fields of vision were investigated and fungal lengths determined by the intersection technique (Olson 1950).

Four replicates from each treatment were used for enumeration of bacteria, protozoa and FDA-active hyphae. Straw (0.05 g wet mass) was homogenized with 5 ml 60 mM sodium phosphate buffer, pH 7.6, for 20 s in a Turrax ultramixer at 25,000 rpm. Bacterial numbers and biomass were estimated in the straw buffer homogenate after staining with acridine orange (Clarholm and Rosswall 1980). Protozoan numbers were estimated (in two of the replicates) in the homogenate by a most probable number method (Darbyshire et al. 1974) using microtiter plates with amoeba saline solution (Page 1967) mixed with washed, pre-grown bacteria as a food source for the protozoa. For estimations of FDA-active hyphae (Söderström 1977) the homogenate was diluted 40 times with phosphate buffer, stained with fluorescein diacetate (10 µg ml^{-1}) and filtered onto a non-fluorescent filter (Millipore black filter, 0.8 µm). Hyphal length was estimated with the intersection technique (Olson 1950) using a Zeiss epifluorescence microscope at 400× magnification. A conversion factor of 3.13 for straw wet mass to dry mass was determined gravimetrically (drying at 40° C for 24 h) from straw moistened and suctioned in the same way as in the main experiment.

A conversion factor of 9.85×10^{-4} was used to convert m fungi to mg fungi (assuming a density of 1.1, a wet to dry conversion factor of 0.15 and an average cross section of the hyphae of $5.97\times10^{-12}\ m^2$ (Wessén 1983)). Individual dry masses used for determining protozoan biomass were 10^{-5} mg for ciliates, 10^{-6} mg for amoebae, and 10^{-7} mg for flagellates (M. Clarholm pers. comm.). A conversion factor of 0.45 was used to determine carbon from dry mass for all organisms, except *F. fimetaria,* for which 0.50 was used (Persson 1983).

Energetics were estimated for the organisms assuming $P/A=0.4$ and $R/A=0.6$ for bacteria and fungi (Heal and MacLean 1975) as well as $P/A=0.2$ and $R/A=0.8$ which were used as annual means in the field by Persson (1983). The energetics quotients used for *F. fimetaria* were $P/C=0.12$, $R/C=0.18$ and $F/C=0.7$, i.e., those for microbivores in Persson (1983).

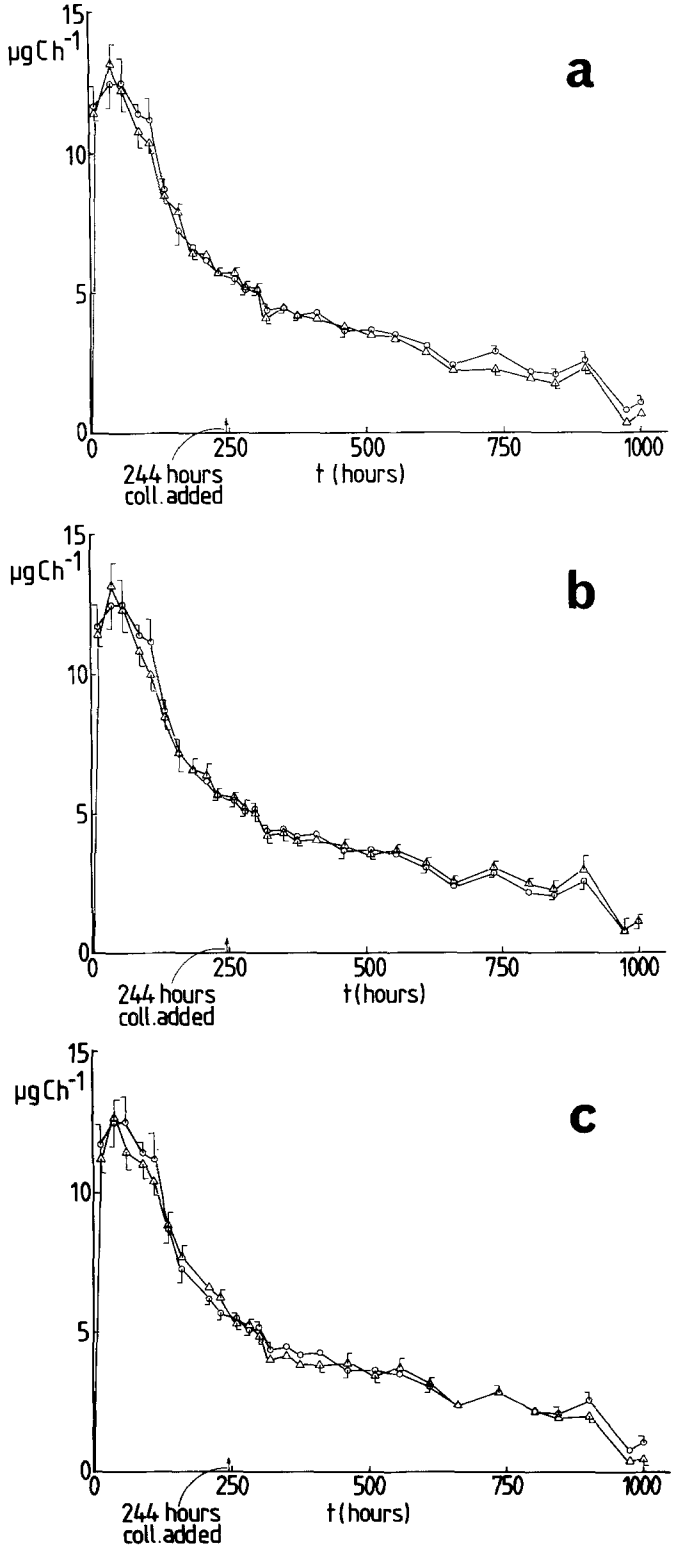

Fig. 2a–c. Microbial respiration (µg C container^{-1} h^{-1}), corrected for calculated collembolan respiration. (No collembola added (○), and 5, 10 and 20 *F. fimetaria* in **a**, **b** and **c**, respectively (△)). Bars indicate one standard error, $n=7$

Results

Microbial respiration (i.e., measured respiration corrected for calculated collembolan respiration) increased rapidly during the first two days and then slowly declined (Fig. 2).

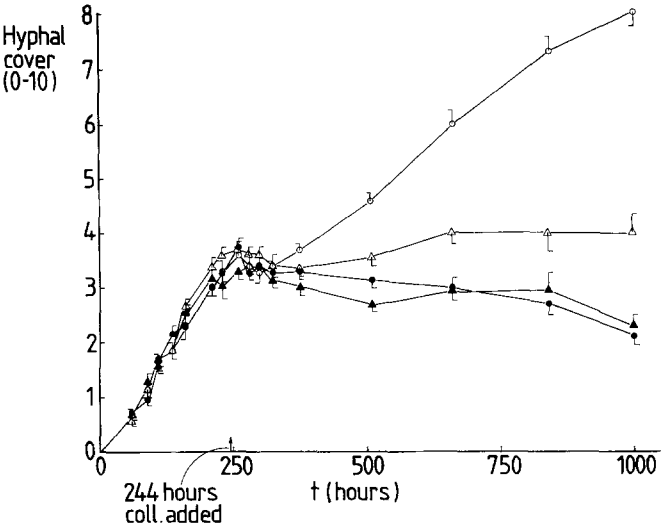

Fig. 3. Surface cover with hyphae. (No collembola added (○), 5 *F. fimetaria* (△), 10 *F. fimetaria* (●), 20 *F. fimetaria* (▲)). The scale used ranges from 0–10, where 0 represents no visible hyphae and 10 represents a total cover with hyphae. Bars indicate one standard error, $n=7$

No differences between grazing levels ($P>0.05$, $n=7$) were found at any time. The possible trends towards the end of the incubation, (respiration in treatments with 5 and 20 collembola < the control and with 10 collembola > the control) did not indicate any consistency in microbial response to increased grazing pressure. No differences between grazing levels were found ($P>0.05$, $n=7$) at any time for the measured respiration, i.e., not corrected for collembolan respiration.

Accumulated microbial respiration, calculated by linear interpolation between samplings and subsequent integration, was nearly identical for the four grazing levels ($n=7$, $P=0.74$ for the whole incubation, $P=0.49$ after addition of Collembola) (Table 1). Average mass loss of organic matter during the incubation was 18.9, 18.3, 20.4 and 17.9% for the containers with 0, 5, 10 and 20 collembola, respectively, but no significant differences ($P=0.14$, $n=3$) were found.

Fungal hyphae on the substrate surface were markedly affected (Fig. 3) by the presence of *F. fimetaria* ($P<0.001$ at $t=508$ h). Shortly after the introduction of Collembola the amount of hyphae decreased in samples containing 10 or 20 collembola, remained nearly unchanged with five collembola and increased steadily in the ungrazed containers until the straw was covered with hyaline hyphae. In the whole substrate, no significant differences ($P>0.05$) in microbial numbers or biomass were found between the grazing levels (Table 2).

The abundance of Protozoa after 1,000 h incubation varied considerably between the two replicates surveyed, and no significant differences ($P>0.05$) were found. The orders of magnitude of the overall mean numbers per g straw dry mass were 10^5, 10^4 and 10^5 for amoebae, ciliates and flagellates, respectively. Two additional containers treated in the same way as the experimental containers were searched for nematodes, but none were found.

The collembola contributed 1% (5 collembola) to 4% (20 collembola) of total respiration after introduction of Collembola (Table 1). The mean numbers of adult *F. fime-*

Table 1. Integrated microbial respiratory sum (mg C container^{-1}), corrected for calculated collembolan respiration. Sum for the whole incubation (1,000 h) and sum for the 756 h after addition of collembola, $n=7$. The calculated collembolan respiration is also indicated. – = standard error not possible to calculate

	0 coll. Mean	S.E.	5 coll. Mean	S.E.	10 coll. Mean	S.E.	20 coll. Mean	S.E.
Microbial respiration (1,000 h)	4.59	0.08	4.49	0.06	4.64	0.20	4.43	0.12
Microbial respiration (756 h)	2.45	0.07	2.36	0.05	2.53	0.14	2.34	0.10
Calculated collembolan respiration (756 h)	0.000	–	0.024	–	0.047	–	0.095	–

Table 2. Fungi, bacteria and collembola after 1,000 h incubation. Units per g organic matter, $n=7$. – = standard error not possible to calculate

	0 coll. Mean	S.E.	5 coll. Mean	S.E.	10 coll. Mean	S.E.	20 coll. Mean	S.E.
Total hyphae ($n=3$)								
(km)	1.4	0.4	0.9	0.2	1.1	0.2	1.2	0.2
(mg dry mass)	1.4	–	0.9	–	1.0	–	1.2	–
(mg C)	0.6	–	0.4	–	0.4	–	0.5	–
FDA-active hyphae ($n=4$)								
(km)	0.23	0.06	0.18	0.05	0.22	0.14	0.17	0.09
(mg dry mass)	0.2	–	0.2	–	0.2	–	0.2	–
(mg C)	0.1	–	0.1	–	0.1	–	0.1	–
(% active)	16	–	19	–	21	–	14	–
Bacteria ($n=4$)								
(No. $\times 10^{-10}$)	3.9	0.7	3.8	0.7	3.4	0.8	3.3	0.4
(mg dry mass)	4.9	1.9	3.6	0.7	3.5	0.6	3.0	0.6
(mg C)	2.2	–	1.6	–	1.6	–	1.4	–
Collembola								
(No.)	0.0	–	70	–	142	–	281	–
(mg dry mass)	0.0	–	0.7	–	1.3	–	2.7	–
(mg C)	0.0	–	0.4	–	0.7	–	1.4	–

taria (9.5 µg dry mass) extracted from the 0, 5, 10 and 20 batches were 0.0, 3.3, 5.7 and 9.6, respectively, indicating a high mortality towards the end of the experiment. The mean numbers of newly hatched individuals (0.3 mm body length) were 0.0, 22.0, 28.3 and 15.0, respectively. Since only a few specimens were found dead in earlier controls and hatching only was observed near the end of the experiment, 0, 5, 10 and 20 collembola per container were used in all calculations.

Discussion

The total respiratory sum for each container, including collembolan respiration, was highly correlated ($r=0.839$, $n=12$, $P=0.0006$) with individual mass losses for each container, indicating good agreement between the two independent methods for measuring carbon loss. Pure carbohydrate $(CH_2O)_n$ metabolism yields 40% of the dry mass loss as C, and 30% of the average mass loss in the present experiment was accounted for in respiratory C. The results from respirometry and gravimetry thus support each other.

In the control, the carbon in bacterial biomass at the end of the experiment was 2.2 mg C g^{-1} and in total fungal mass, 0.6 mg C g^{-1} (cf. Table 2). Protozoan biomass contained about 0.1 mg C g^{-1}. The respiratory sum was 64 mg C g^{-1}. Using the energetic quotients given by Heal and MacLean (1975), this corresponds to a microbial production of 43 mg C g^{-1}, equivalent to a 15-fold turnover of the microbial biomass in relation to the final biomass. Using the energetic quotients given by Persson (1983), the microbial production becomes 16 mg C g^{-1} organic matter, equivalent to a six-fold turnover.

The high turnover of microbial biomass obtained using two sets of widely different energetic quotients (cf. Heal and MacLean 1975; McGill et al. 1981; Persson 1983) is not necessarily similar for bacteria and fungi. In the control very little fungal grazing can be expected. Amoebal grazing cannot be excluded, since mycophagous amoeba are found in a wide range of soils (Chakraborty et al. 1983). However, amoebae feed by puncturing the hyphal walls and sucking out the cytoplasm, and the empty cell walls, if not further decomposed, would still be included in estimates of total hyphal length. On the other hand, the amount of FDA-active hyphae would be reduced by heavy amoebal grazing. The fraction FDA-active/total hyphae was, however, comparatively high and similar between treatments at the end of incubation (Table 2), which would indicate that the fungi in all treatments were not subjected to a high amoebal grazing pressure. Since fungal cell walls are resistant to decomposition (Hurst and Wagner 1969) even cell walls emptied early during incubation may have been included in the total count. Thus, the total fungal mass present after incubation in the control can be regarded as a minimum estimate of fungal production during the experiment.

Bacterial production, on the other hand, probably was subjected to grazing by protozoa even in the control. Amoebae, ciliates and many flagellate species readily consume large amounts of bacteria (Heal and Felton 1970; Habte

and Alexander 1977) and ciliates can consume amoebae. Within this complex food web both bacteria and amoebae may have reproduced throughout the incubation, turning over several times.

The ratio between bacterial and fungal biomass was high compared with that found in a field experiment with barley straw litter-bags incubated 15 cm below ground under barley (Andrén et al. unpubl.). When the barley straw in the field experiment had lost 20% of its original mass, total hyphal length was 1 km, similar to that found in the present experiment, but bacterial biomass was one order of magnitude lower and amounted to 0.5 mg. The grinding of straw before the laboratory experiment probably accounted for part of this difference, since a large surface to volume ratio is crucial for bacterial attack, whereas the fungi may have a competitive disadvantage when colonizing a ground and densely packed substrate (Hanlon 1981b). Moisture conditions were not considerably different, water content was about 68% of the wet mass in the laboratory experiment and ranged from 50 to 67% during the two-year field experiment (Sohlenius and Boström 1984). The absence of bacterial-feeding nematodes in the laboratory experiment could also have affected the difference between laboratory and field experiments, since they were abundant in the field experiment (Sohlenius and Boström 1984) and nematodes can have a strong influence on bacterial abundance and activity (Anderson et al. 1978; Bååth et al. 1981).

The fungal contribution to respiration, calculated using the two set of energetic quotients (Heal and MacLean 1975; Persson 1983), then ranges from 1.4% to 3.8% of the total respiration. Protozoa and bacteria thus accounted for more than 95% of the respiration.

The collembolan biomass increase during the experiment was 3.6 μg C individual^{-1}. Using the energetic quotients from Persson (1983), production, respiration, consumption and defecation for the 20 collembola treatment was calculated as 1.0, 1.5, 8.4 and 5.9 mg C g^{-1} organic matter, respectively. Thus the collembola in this batch consumed 20%–50% of the microbial production, depending on the set of quotients used.

Many Collembola are considered to be fungivorous (Christiansen 1964; Petersen 1971; Hågvar and Kjöndal 1981; Petersen and Luxton 1982). Through microscopical examination we found hyphal fragments and fungal spores in the guts of *F. fimetaria* after incubation. However, Bödvarsson (1970) found that soil-inhabiting collembolan species had a lower percentage of hyphae in their guts than surface-living species. *F. fimetaria* is a soil collembolan, and in laboratory cultures this species may gnaw directly on straw surfaces, making 'ditches' in it, possibly grazing on surface bacteria (J. Lagerlöf pers. comm.). Plant material ingestion has also been observed by Dunger (1956), who found that an adult *F. fimetaria* consumed 0.049 mm^3 of decomposing leaf material per day at 18° C. The leaves were not sterilized and the collembola may have mainly assimilated microorganisms. Ulber (1983) observed that this species did not consume live sugar beet roots, except for parts heavily infected with the plant pathogenic fungus *Pythium ultimum*, which was significantly reduced by the collembolan grazing. In conclusion, *F. fimetaria* may be described as an unspecialized microbial feeder.

If it is assumed that the collembola only consumed fungi, they would have consumed 14 times the total fungal production in the 20 collembola treatment, without giving any significant differences in fungal biomass at the end of the experiment. Even though 70% of the consumption is disposed of as faeces, in which hyphal parts may still be recognized (Vannier 1979), it is highly unlikely that this was the case. However, the observed reduction in surface hyphae may fall within the limits of error in the estimates of total hyphae, especially since the highest estimate was found in the ungrazed control.

Our hypothesis is that the collembola grazed on the surface hyphae, but that their main food source was the bacteria and protozoa, which accounted for most of the microbial production. The trend towards lower bacterial biomass with increasing collembolan numbers (Table 2) also suggests bacterial consumption by the collembola. *F. fimetaria* thus competed with the protozoa as grazers on the bacteria, which turned over rapidly in all treatments. The collembola also ingested protozoa and reduced protozoan grazing to some extent, not detectable with the methods used.

In conclusion, the results obtained in simple microcosm experiments should be viewed with caution when extrapolating to the field situation. More complex and natural laboratory microcosms, that can be maintained for a longer time, include several generations of collembola and, e.g., gamasid predators may provide a more rewarding approach. Careful calculations of energy and nutrient flows, based on field abundances of microorganisms, grazers and predators is another, perhaps too little used, approach that can estimate the effects of collembola and other soil animals on decomposition and nutrient cycling (Persson et al. 1980; Elkins and Whitford 1982; Persson 1983) and create useful hypotheses to test in future experiments.

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O. Andrén was responsible for the design of the experimental containers, the gas chromatographic measurements and the compilation of results. J. Schnürer was responsible for the microbial estimates. Both authors are equally responsible for the experimental planning and research conclusions.

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