



The impact of soil compaction on euedaphic Collembola

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Abstract

Tillage operations and field traffic may cause soil compaction and alter the pore characteristics in soil. These practices often lead to a reduction in habitable pore space for the soil mesofauna. In the present study the abundance of some euedaphic species of Collembola was investigated under a range of soil bulk densities normally found in agricultural soils. The study was performed using containers with defaunated soil that was compressed to six levels of bulk density in the range 1.02–1.56 g cm⁻³. One of the following species was added to a separate series: *Mesaphorura macrochaeta*, *Protaphorura armata*, and *Folsomia fimetaria*. The number of individuals and the concentration of ergosterol (used to estimate fungal biomass) were measured after each experiment and related to bulk density and pore size distribution. A series of experiments in which straw was added to the soil in order to increase microbial life was also included. Only *F. fimetaria* was used in the straw amended series. In the soil experiments without straw amendments, the numbers of *M. macrochaeta* and *P. armata*, were significantly reduced when bulk densities increased from 1.37 to 1.47 g cm⁻³. *F. fimetaria* did not exhibit any significant response to compaction. The ergosterol concentration was independent of bulk density. When straw was added, the abundance of *F. fimetaria* declined significantly with increasing bulk density from 1.21 g cm⁻³. The decline in collembolan numbers was probably due to the decline in coarse pores (>120 μm) because the ergosterol concentration was independent of bulk density. These results show that soil structure and decline in habitable pore space are the key parameters in the abundance of euedaphic Collembola in soil. © 2003 Elsevier B.V. All rights reserved.

Keywords: Euedaphic Collembola; Soil compaction; Habitable pore space; Fungal biomass; Specific pore volume

1. Introduction

In agricultural soils the densities of Collembola range from less than 10 000 to 120 000 individuals per square meter i.e. ind m⁻² (Axelsen and Thorup-Kristensen, 2000; Christensen et al., 1987; Filser and Fromm, 1995). The majority of these animals are found in the upper (0–10 cm) layer, depending on habitat type, although some species are evenly

distributed in the entire plough layer (Christiansen, 1964).

The abundance of Collembola in arable soils is closely linked to soil structure and functions (Usher, 1975). Collembola are not able to make their own burrows and are entirely dependent on air-filled pores that are dimensioned to at least their body width. They tend to avoid narrow pores, probably in order to protect their wax coat against damage (Choudhuri, 1961). The extent to which Collembola are able to access and inhabit pores in the soil is determined by the following aspects of soil physical conditions: (1) the volume of habitable pore space, (2) connectivity of these pores,

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and (3) moisture and temperature regimes (Didden, 1987; Hopkin, 1997; Joesse, 1981).

These parameters and the size of the Collembola and how they behave and respond to soil conditions in general are fundamental for abundance and species composition (Chagnon et al., 2000). This implies that habitable pore space for collembolans is not only the space that exceeds the width and length of the animal, but also an environment in which the animal is able to develop all of its characteristic features.

Very few studies have focused on collembolan abundance with soil porosity as the only variable. In a container study with *Protaphorura fimata* (Gisin), Didden (1987) demonstrated that juveniles did not show a preference for being in either loose (9.3% of pores >300 μm) or dense (5.6% of pores >300 μm) soil, while larger animals showed a significant preference for loose soil even though the dense soil did contain habitable pore space. Haarløv (1960) conducted another study of the interrelationships between soil pores and microarthropods (including Collembola), in this case under field conditions, and concluded that smaller animals tended to be dominant in habitats or layers with small average pore sizes.

Correlations between an increase in soil bulk density caused by wheeling and tillage and reduction in abundance of euedaphic Collembola and species diversity have been found in past studies (Dittmer and Schrader, 2000; Heisler and Kaiser, 1995; Schrader and Lingnau, 1997). Quantification of the effect of soil structure and habitable pore space per se on collembolan abundance has, however, not yet been performed. When the relationship between soil structure and abundance of Collembola is investigated under field conditions, parameters other than habitable pore space influence abundance, such as weather conditions and the effects of tillage. In the present study the influence of soil compaction on collembolan

abundance was investigated in a controlled environment in order to reduce the influence of parameters not directly related to habitable pore space. The soil structure was altered by compaction in order to quantify how changes in habitable pore space affected the abundance of some euedaphic collembolan species.

2. Materials and methods

2.1. Experimental design

The different treatments are listed in Table 1. The experiment was set up in containers in which defaunated and restructured soil (labeled NA for non amended) was compressed to a range of bulk densities normally found in arable soils (Table 2). Restructured soil was used rather than undisturbed soil cores in order to reduce variation between the containers. Euedaphic, juvenile Collembola, *Mesaphorura macrochaeta* (Rusek), *Protaphorura armata* (Tullberg), and *Folsomia fimetaria* (L.), were added to the top of the soil cores after compression. These three species were selected because they are euedaphic and occur naturally in the agricultural field where the soil was collected, and they cover a broad range of body sizes (Fig. 1). The use of juveniles instead of adults ensured that the reproductive output truly reflected the accessible food base, as adults might carry reserves from the cultures for the production of eggs. Size distribution of pores was estimated on the basis of water retention in a separate series with soil without Collembola. The containers were incubated for 63 or 64 days, respectively.

An additional series of containers was created in which straw was incorporated (labeled SA for straw amended). This was done in order to increase the quantity and quality of the food base for Collembola in

Table 1
The starting conditions of the different treatments

Code	Treatment	Species	Number of juveniles added	Number of replicates	Incubation time (days)
NA-M	No amendments	<i>Mesaphorura macrochaeta</i>	100	7	63
NA-P	No amendments	<i>Protaphorura armata</i>	30	7	63
NA-F	No amendments	<i>Folsomia fimetaria</i>	75	7	64
SA-26	Amended with 1.05% straw	<i>Folsomia fimetaria</i>	75	6	26
SA-61	Amended with 1.05% straw	<i>Folsomia fimetaria</i>	75	6	61

Table 2
Bulk densities in the different soil treatments

Compaction treatments	Surface load (kPa)	Bulk density (g cm^{-3})		
		Soil drained in sandbox ($n = 4$)	Soil without amendments ($n = 21$) (NA)	Soil with straw amendments ($n = 12$) (SA)
I	13.5	1.18	1.10	1.02
II	27.1	1.27	1.19	1.12
II	54.1	1.32	1.28	1.21
IV	108.3	1.37	1.37	1.31
V	216.5	1.43	1.47	1.40
VI	433.1	1.50	1.56	1.50

In each container 290.0 g of soil (± 0.5 g) was added; soil surface area was 55.4 cm^2 . The bulk density is the mean of the replicates for each compaction treatment.

comparison to the series without amendments. In order to reduce labor intensity only *F. fimetaria* was used in this series and size distribution of pores was not determined. *F. fimetaria* was selected for the SA series because of its medium size. The SA series was split into two-time series, 26 and 61 days, respectively in order to follow the succession of *F. fimetaria* and fungal biomass.

Since the microbial community was not controlled, measurements of fungal biomass were also included because fungi are an important food source for the genera used in this experiment (Bödvarsson, 1970; Hanlon and Anderson, 1979; Kaneko et al., 1998). Ergosterol, a cell membrane compound specific to

fungi was quantified to estimate fungal biomass (Montgomery et al., 2000; Stahl and Parkin, 1996).

2.2. The soil containers

2.2.1. Soil

The soil was collected in May from the 5 to 10 cm layer of an organically farmed field at Rugballegaard Experimental Station near Horsens, Denmark. Immediately after field sampling the soil was defaunated by three cycles of freezing (24 h at -18°C) and thawing (36 h at 22°C). The soil was homogenized by sieving (8 mm wire gauze sieve). The basic characteristics of the soil (0–20 cm depth) were as follows:

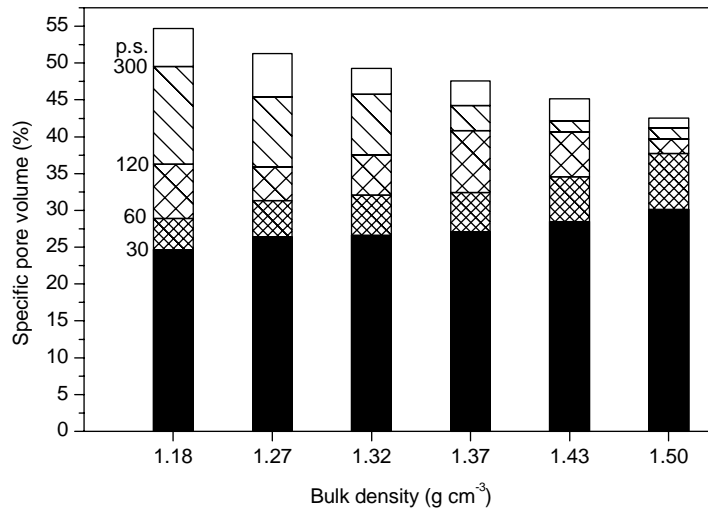


Fig. 1. Specific pore volume in soil without amendments and collembolans (soil cores drained in sandbox). Each column represents the mean of four replicates. The numbers below 'p.s.' indicate tube equivalent pore diameter in micro meter.

10.3% clay, 14.7% silt, 12.9% coarse silt, 27.8% fine sand, 30.7% coarse sand, 3.6% organic matter, particle density 2.608 g cm^{-3} , 0.18% total N, 2.10% total C (Axelsen, unpublished results). The water content was 18% (w/w).

2.2.2. Straw amendment

In the treatments with straw amendment, organically grown wheat straw was chopped into pieces measuring approximately 1 cm and dried for 24 h at 40°C . The straw was divided into 2.5 g portions and soaked in 4.5 g water for 24 h. Each portion was homogeneously mixed with soil from each container. The amount of straw added constituted 1.05% (w/w) of the soil, which approximately corresponds to incorporation of 10 tons of wheat straw per hectare in the upper 7 cm of soil (at 1.35 g cm^{-3}).

2.2.3. Containers

The containers (8.4 cm diameter and 5.5 cm height) were made of transparent acrylic tubes that were closed at both ends with lids. In order to seal the containers, pieces of parafilm (1 by 6 cm) were stretched along the edges of the tubes before they were closed with lids. A 1 cm^2 hole was made in the top lid so that air could circulate. The hole was closed with $45 \mu\text{m}$ nylon mesh to prevent the Collembola from escaping.

2.2.4. Soil compression

290 g of soil (fresh weight (FW), $\pm 0.5 \text{ g}$) was added to each container. Surface pressure was applied uni-axially for 2 min to the top of the soil with a piston of approximately the same diameter as the container. The loads were controlled by a pressure transducer and amounted to 13.5, 27.1, 54.1, 108.3, 216.5, and 433.1 kPa for the six series of compaction treatments, respectively (Table 2).

The post-compression height of the soil column was measured and the volume of soil calculated by multiplying the height by the cross sectional area of the container. Soil-water content was determined from a sub-sample, which then allowed calculation of soil-bulk density.

The bulk densities ranged from 1.10 to 1.56 g cm^{-3} in NA and 1.02 to 1.50 g cm^{-3} in SA (Table 2). The bulk densities in the soils used for determination of the pore size distribution ranged from 1.18 to 1.50 and were in a narrower range than the NA series (Table 2).

2.2.5. Pore size distribution

A series of containers with compacted soil (NA) was made for estimating the pore size distribution. The soil samples were saturated with water in a sandbox and subsequently drained under tensions corresponding to tube-equivalent pore diameters of 30, 60, 120, and $300 \mu\text{m}$, respectively (Schjønning, 1985).

In order to allow comparisons of soil-pore volumes across the series with different bulk densities, specific pore volume (Φ_{sp}) of a given pore size class was calculated as follows:

$$\Phi_{\text{sp}} = \frac{W\psi}{(m_x/\rho)}$$

$W\psi$ (cm^{-3}) is the volume of water drained between two tensions. The denominator of the formula is the volume of the soil particles where m_x (g) is the mass (xeromass) of oven-dried soil, and ρ (g cm^{-3}) is the particle density. Total soil porosity may easily be obtained from the volume of soil particles (the denominator in the equation) and was used in the calculation of the volume of pores $>300 \mu\text{m}$. The specific pore volume (Φ_{sp}) was multiplied by 100 in order to express the fraction as a percent.

2.3. Faunal treatments

2.3.1. Addition of Collembola

The three species of Collembola (*Mesaphorura macrochaeta*, *Protaphorura armata*, and *Folsomia fimetaria*) were taken from laboratory cultures. Each species was added to the top of the soil cores in the numbers listed in Table 1. Juveniles were used in all treatments. The cultures of *F. fimetaria* were synchronized to be between 7 and 14 days old (Krogh, 1995). The juveniles of the other two species were not synchronized, as there were no laboratory procedures for synchronization.

The containers were kept in boxes lined with foam rubber that were sprayed with water once a week in order to keep the air saturated. The lids for the boxes were only partially closed so that air could circulate. The temperature remained constant at 20°C . Water was not added to the containers because the total loss of water per unit was less than 0.5 g.

2.3.2. Extraction of Collembola

Before extraction of Collembola, all soil cores were carefully broken into smaller fragments and transferred to smaller containers (6 cm diameter) that could fit into the high-gradient extractor. The extraction was performed by gradually increasing the temperature over a 5-day period, from 30 °C on day 1 to 60 °C on day 5. At the bottom of the extractor the temperature was kept at 5 °C (Krogh, 1995). After the extraction the Collembola were frozen at –18 °C.

2.3.3. Collembolan measurements

One hour before counting, the containers with Collembola were taken out of the freezer and 40 ml of 70% ethanol was added. The Collembola were subsequently collected with a small strainer (1.5 cm diameter, 80 µm steel mesh,) leaving sand and other particles in the container. Ethanol was used to rinse the Collembola off the strainer, through a funnel and into a Petri dish. When there were less than approximately 100 individuals in a Petri dish the Collembola were counted under a microscope. Otherwise a picture of each Petri dish was taken with a digital camera attached to the microscope. The counting was then done manually using a photo-editing program.

For measuring the width (widest cross-section) and length (head-to-tail) of Collembola, images of the animals were analyzed in Image-Pro Plus 4.0. Only pictures of living laboratory animals were used.

2.4. Ergosterol analyses

Approximately 4 g soil (FW) samples were taken for ergosterol analysis and stored at –18 °C for 3 to 6 months before analysis. Only soil from treatments with *F. fimetaria* (NA-F, SA-26, and SA-61) was analyzed. The procedure described by Larsen et al., (2004) was used for extraction and quantification.

In samples of soil with straw amendments, straw and soil were separated because the amount of straw was unevenly distributed in the different samples. Because the weight loss of straw during decomposition was not measured in this study the weight loss was estimated from values obtained by Bowen and Harper (1990) in a study of decomposition by cellulolytic fungi of wheat straw. The straw biomass was estimated to constitute 0.81% (23% weight loss) of the total soil mass after 61 days. The concentration of ergosterol

in each container was calculated according to these fractions.

2.5. Statistical analyses

All statistical analysis was performed using Stat Graphics Plus 4.0. For treatments in which the variances were similar at the 95% confidence level, Fisher's least squares difference procedure (FLSD) was used to discriminate among the means that were significantly different at the 5% level. For treatments in which FLSD could not be used, Kruskal–Wallis tests were employed. When medians were different at the 95% confidence level, median notches were added to the box plots to determine which medians were different. For comparing two samples *t*-tests were used when means were equal (<5%). All correlations between variables were significant at $P < 0.01$.

3. Results

3.1. Soil data

The volume of coarse pores (pores >120 µm) decreased considerably with increased bulk densities. In compaction treatments V and VI pores >120 µm constituted 9.4 and 6.6%, respectively, of the specific volume as opposed to 33.8% in compaction I (Fig. 1).

The bulk density accounted for 95.1% of the variation in the specific volume of pores >120 µm ($r = -0.97$, $df = 23$).

3.2. Ergosterol

There were no effects of bulk density on ergosterol concentrations in the NA-F, SA-26, and SA-61 treatments. The mean values of ergosterol in the NA and SA treatment were 0.96 and 2.94 µg g⁻¹ dry soil, respectively.

3.3. Faunal treatments

About 83% of *F. fimetaria* from laboratory cultures were estimated to be smaller than 0.30 mm in width, and about 10% were smaller than 0.12 mm. All *M. macrochaeta* from laboratory cultures were smaller

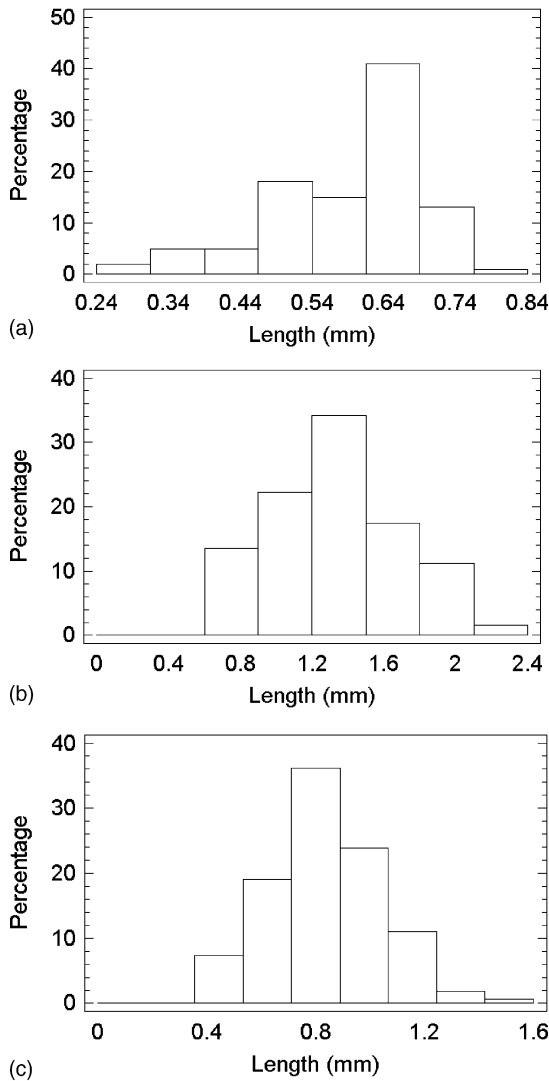


Fig. 2. Distribution of length of juvenile and adult Collembola from laboratory cultures. (A) Length of *M. macrochaeta* ($n = 99$). (B) Length of *P. armata* ($n = 126$). (C) Length of *F. fimetaria* ($n = 163$). The animals were fed baker's yeast and cultured on plaster of Paris and charcoal.

than 0.22 mm in width, and about 30% were smaller than 0.12 mm. Twenty five percent of *P. armata* from laboratory cultures were smaller than 0.30 mm in width. The distributions of the lengths are displayed in Fig. 2.

In the series with *M. macrochaeta* (Fig. 3A) and *P. armata* (Fig. 3B) in soil the number of individuals was significantly lower in compactions V and VI than

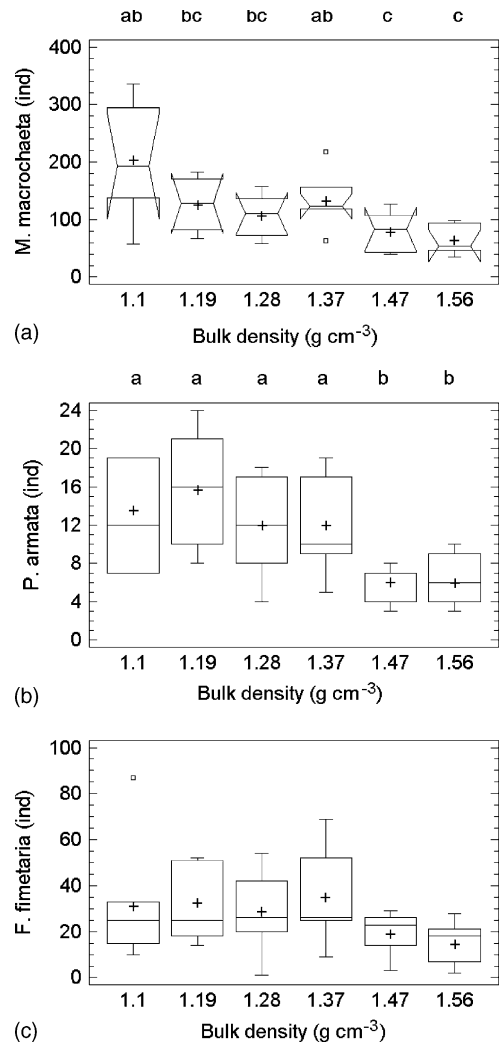


Fig. 3. Individuals per container in NA. (A) *M. macrochaeta* after 63 days in NA ($n = 7$). Kruskal–Wallis: $P < 0.01$. (B) *P. armata* after 63 days in NA ($n = 7$). FLSD: $F = 5.22$, $P < 0.01$. (C) Individuals per container of *F. fimetaria* after 64 days in NA ($n = 7$). FLSD: $F = 1.52$, $P = 0.21$. Median, 25th and 75th percentiles, lowest and highest observation, means [+], outliers (C) and median notch (A). If the median notch intervals (uncertainty intervals for the medians) do not overlap, there is a statistically significant difference between two medians at 95% confidence level. Different letters indicate significant differences.

compaction I. No significant effect of compaction was seen with *F. fimetaria* in soil (Fig. 3C). Here the mean number of individuals was 26.8 per container (4842 ind m^{-2}), a drop of almost 50 from the initial number of 75 per container (13534 ind m^{-2}). In the treat-

ments with *P. armata* there was a drop from the initial numbers of 30 to 13.3 (2403 ind m⁻²) individuals per container in compactions I–VI and 6.0 individuals per container in compactions V and VI (1082 ind m⁻²). The treatments with *M. macrochaeta* were different in that they showed an increase from the initial number of 100 to 142.4 (25 681 ind m⁻²) individuals per container in compactions I–IV. In compactions V and VI there were 70.4 (12 706 ind m⁻²) individuals per container.

In the series with straw amendment, where only *F. fimetaria* was used, the mean number of individuals in the different compaction treatments was 10 to 30 times higher when compared to the NA-F series. There was no significant difference between SA-26 and SA-61 under similar levels of compaction (*t*-test: *P* > 0.05). There was a progressive decline in individuals with increasing bulk densities as 71.40% of the variability in abundance can be explained by bulk density when two unusual residuals are excluded (*r* = 0.84, *df* = 26). After 26 days, compactions I and II had a mean of 747.5 individuals per container (134849 ind m⁻²), which was significantly more than compactions IV–VI with 238.1 individuals per container (42 947 ind m⁻²). After 61 days compactions I and II contained 835.8 individuals per container (150820 ind m⁻²) and had significantly more individuals than compactions V and VI with 184.4 individuals per container (33 275 ind m⁻²).

4. Discussion

All three species of Collembola responded with a decline in the number of individuals to a decrease in the volume of coarse soil pores. This is in agreement with results from field experiments that showed negative correlations between collembolan abundance and compaction (Dittmer and Schrader, 2000; Heisler and Kaiser, 1995; Schrader and Lingnau, 1997). The bulk densities used in this experiment were close to values normally found in agricultural fields. Compactions I–IV corresponded to the changes in the surface layer (0–4 cm) before and after tillage in the field where the soil was sampled (Axelsen, unpublished results). In September the bulk density in that field was 1.35 g cm⁻³, and during mouldboard ploughing 2 weeks later it dropped to 1.05 g cm⁻³. The soil settled to 1.17 g cm⁻³ after another 2 weeks

and was 1.32 g cm⁻³ 5 months later in March. In the 8–12 cm layer the bulk densities were around 1.35 to 1.40 g cm⁻³. The highest bulk density in this experiment, 1.56 g cm⁻³ in compaction VI in NA, corresponded to compaction in wheel tracks in the surface layer (Munkholm et al., 2002).

The animals in this experiment were not exposed to mechanical stress, which is often the case in the field. In the field the collembolans are already below ground when compaction occurs whereas the collembolans in this experiment entered the soil from the surface after compaction. The experiment does, however, reflect the available food base for collembolans under various bulk densities.

The species used were expected to respond differently to increased bulk density because of their different body sizes. The most notable difference between *M. macrochaeta*, *F. fimetaria* and *P. armata* was that that *M. macrochaeta*, in contrast to the two other species, actually reproduced beyond initial numbers in loose soil. In the series with straw amendments and *F. fimetaria* the effect of compaction on abundance was significant at lower bulk densities than in soil. From the knowledge gathered from past investigations and observations this correlation between abundance and bulk density was to be expected, yet it had not been quantified as in the present study.

The mortality of *P. armata* and *F. fimetaria* in soil might also be caused by a low nutritional value of the fungal community (Jørgensen, 2002) or a lack of other nutritious carbon sources. *M. macrochaeta* did adapt more successfully to soil than the two other species. This might either be because this species, with its small body size, was able to (1) forage in smaller pores or (2) because this deeper-dwelling species might be better adapted to the utilization of different or less nutritious food than *F. fimetaria* and *P. armata*. Van Amelsvoort et al. (1988) have, for instance, reported that *Mesaphorura krausbaueri* s.l. feed on bacteria, while experiments conducted by Shaw (1985) indicate that fungi probably constitute the main diet for *P. armata*. *F. fimetaria*, on the other hand, feed on fungi as well as bacteria and probably protozoa (Andrén and Schnürer, 1985), but its mortality in even loose soils and its lack of response to compaction suggest that this species has different food requirements to *M. macrochaeta*.

Soil pore pathways are not uniform in structure and diameter, and the neck of pores may probably often be

a limitation for Collembola as shown here. The width or height of the animals regulate which pore sizes they can access, while the entire size and idiosyncrasies specific to a species or age group limits habitable pore space (Didden, 1987; Faber and Joosse, 1993). In an investigation of vertical distribution of litter dwelling Collembola in a coniferous forest, Faber and Joosse (1993) found that adults of most species were located higher up in the soil profile, while hatchling and juveniles generally were captured in lower layers. Vertical distribution patterns could not be predicted from body length, however, as the relationship of body length to mean relative depth varied among species.

Restructuring and compression homogenizes the soil more than field ploughing and thereby diminishes the fraction of coarse pores relatively more (Schjønning et al., 1999). Identical regression lines were found between pores $>120\ \mu\text{m}$ in this mesocosm experiment and pores $>300\ \mu\text{m}$ in an experimental field from the soil collecting site (Axelsen, unpublished results). Schjønning et al. (1998, 1999) found a similar pattern in a comparison of a disturbed soil with an undisturbed one. The modified soils, even after a 17 month period of structural regeneration under field-like conditions, had a pore system with relatively small pores enmeshed in the soil matrix, whereas the undisturbed soil exhibited larger and continuous pores. In disturbed soils, the connectivity between pores is affected by physical disruption. In undisturbed soils, pores tend to be more interconnected because they are produced by roots, soil fauna, and natural cracks rather than by mechanical pressure (Schjønning et al., 1998, 1999). The soil in this experiment can be considered to be heavily fractionated and disturbed, exhibiting randomly scattered macro pores. In light of this and the small volume of coarse pores in compaction treatments V and VI, it must be assumed that the animals in these treatments mainly foraged on top of the soil. During the experiment we also observed that when the animals were exposed to light/heat they were only to some extent able to escape from the surface in compaction V and not at all in compaction VI, but the animals reappeared on the soil surface after a few minutes. In the loose soils the animals rarely reappeared on the soil surface. The relatively high numbers of *F. fimetaria* in SA in compact soils ($>30\ 000$ animals per square meter) were due to the food (pieces of straw) that was present on the soil

surface. The pieces of straw on the surface were not removed after compaction because this would rearrange the soil particles on the surface (loosen the soil).

The necks of pores are decisive for Collembola and access to the pore system is adequately addressed when applying the water retention technique, as in this study. We advocate this approach also for further studies; however, we also suggest the use of techniques such as image analyses of thin soil sections as well as investigation of the connectivity between soil pores. The combined use of air diffusivity and permeability measurements may be another relevant tool for the description of the pore system (Schjønning et al., 2002). More concise estimates of the soil volume available for collembolan under different structural regimes are needed.

5. Conclusions

Our study shows that an increase in bulk density decreased collembolan abundance. It appeared that the effect of compaction on abundance was most pronounced when the food base was relatively large. There was a significant effect on *F. fimetaria* abundance at bulk densities similar to field bulk densities few weeks after tillage. At the bulk density compared to that in a wheel track the abundance was about one-fifth of that in the loose soil. The effect of compaction is most likely due to a decrease in habitable pore space, as the fungal biomass did not decrease with compaction. The results also suggest that compaction affects the function performed by the collembolan community adversely as the smallest of the species in the study, *M. macrochaeta*, was reduced significantly with increase in bulk density.

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