

Effects of fertilisation and edaphic properties on soil-associated Collembola in crop rotation

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Abstract. In this study, the Collembola population and their seasonal fluctuations were measured on light-textured field soils (Cambic Arenosol and Stagnic Luvisol) in Southern Estonia. A ten-year-old field experiment with potato and spring cereals in crop rotation under different fertilisation was the main sampling area. Additional research was carried out on sandy soils cropped with spring barley. There was also considerable but not drastic variation in chemical topsoil parameters between treatments and sites. Modified Mcfayden equipments were used to extract Collembola from soil samples. The average quantities of Collembola varied within the range of 700–14 300 and 0–600 individuals m^{-2} for the eudaphic and hemiedaphic group, respectively. Application of organic manure and mineral nitrogen induced an increase in Collembola populations but the differences between treatments remained insignificant. The abundance of euedaphic Collembola under spring barley in September was several times higher than under potato. The influence of crop and probable amount of roots on the abundance of Collembola was more pronounced than that of fertilisation or soil texture and chemical features. It was hypothesised that the euedaphic Collembola community is subjected to density dependent regulation, despite significant year-to-year changes towards the end of the growing season.

Key words: Collembola, cropping, fertilisation, seasonal change, soil texture

INTRODUCTION

Modern agriculture requires more active human intervention in the soil ecosystem and better understanding of how to direct soil processes for environmentally friendly agronomic practices. According to Odum (1969), protectiveness of natural ecosystems can be characterised, besides other factors, by closed nutrient cycles, high energy efficiency entering into system, high species diversity, high biological stability and numerous occurrences of symbiosis. Collembola are, together with mites, the dominant arthropods in soils (Petersen & Luxton, 1982). Collembola enhance nutrient and plant nutrient uptake in laboratory experiments (Mebes & Filser, 1998), as well as in grassland ecosystems (Bardgett and Chan, 1999). Several studies have recently shown that Collembola can be considered as omnivorous, not just selective fungi feeders, and, moreover, they are able to suppress pathogenic nematodes (Gilmore & Potter, 1993; Hyvönen & Persson, 1996; Rusek, 1998). Thus monitoring the abundance of these soil organisms in agroecosystems could give us useful information on the sustainability of different soil management systems.

Collembolans have long been recognised as an interesting insect group in agricultural fields (e.g. Müller & Rauhe, 1959). Agronomic activities destabilise the entire soil ecosystem and, moreover, soil cultivation physically rearranges habitats. Many causal connections have been established between Collembola, the cropping systems and environmental factors (Lagerlöf & Andren, 1991; Krogh, 1994; Butz-Strazny, 1996; Wardle et al., 1999; Dittmer & Schrader, 2000), although in most studies contrasting soil management was used for comparison. Field studies dealing with Collembola have been recently conducted also in tropical agriculture (Bandyopadhyaya et al., 2002; Culik et al., 2002). There is still a lack of experimental evidence as to whether Collembola acts as a bioindicator or as an opportunistic organism in crop rotation under conventional soil management. In view of the extensive literature on Collembola distribution in ecosystems, it is remarkable that their relationship with physical and chemical soil properties have remain comparatively unexplored. Some effort to fill these gaps has been recently made with respect to forest soils (Chagnon et al., 2000).

The aims of this study were: to study in a 10-year-old crop rotation experiment how ecological groups of Collembola respond to different fertilisation schedules and annual climatic conditions. Potato field was selected for extensive research, because of autumnal manure application. Additional studies have been conducted to investigate the influence of soil texture and vertical distribution on Collembola abundance under spring barley.

MATERIALS AND METHODS

Study area and climate

The main research field was situated near Tartu (26°40'E; 58°22'N) and the second site was at Koorvere (26°58'E; 58°08'N).

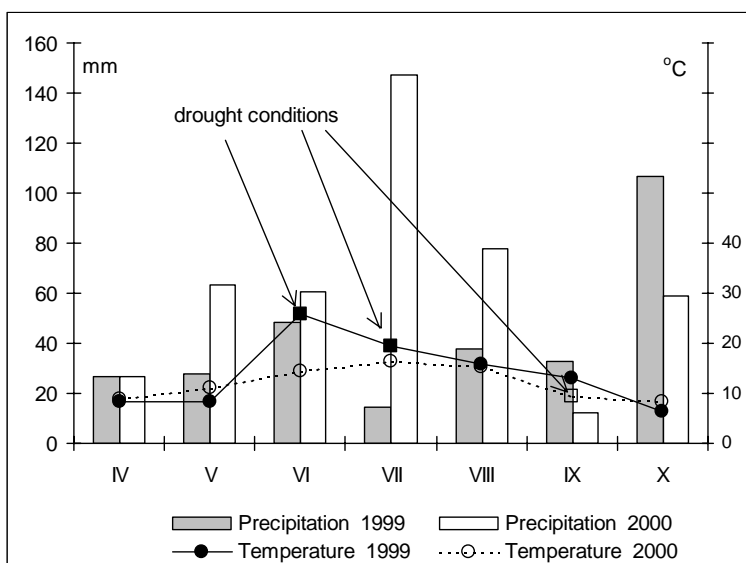


Fig. 1. Walter's climatic diagram for the growing seasons in Tartu in 1999–2000.

Table 1. General properties of topsoils.

Site <i>Soil (WRB)</i>	Texture %			Bulk density	Porosity	Specific surface	Corg	C/N	pH KCl
	clay	silt	sand	g cm^{-3}	%	$\text{m}^2 \text{g}^{-1}$	g kg^{-1}		
Koorvere									
<i>Cambic Arenosol</i>	0.2	14.0	85.8	1.60	35.7	33.2	10.1	12.6	7.3
Tartu									
<i>Stagnic Luvisol</i>	8.5	32.1	59.4	1.52	37.1	33.3	9.5	10.0	6.0

In Southern Estonia the average annual air temperature is close to 5°C and precipitation there remains around 600 mm. The climatic data collected over the course of the study were summarised in Walter's climate diagram (1955). This climate diagram (Fig. 1) has been based on the assumption that 20-mm precipitation is scaled equal to 10°C. The equality of precipitation and temperature on this scale illustrates hydrothermal conditions for soil-plant ecosystems in a temperate climate. If the local temperature curve rises above the rainfall column, it means a higher evaporation rate and intensive topsoil drying for the site. Overall, the Estonian summer is humid with a few drought periods. The summer in 1999 can be considered as normal; in 2000, the summer was unusually rainy.

Fields

The main study was carried out during two consecutive years (1999–2000) on the International Organic Nitrogen Long-Term Fertilisation Experiment (IOSDV in German) established in Tartu in 1989. The Tartu trial is the northernmost of a series of field experiments across Europe (Kuldkepp et al., 1996). The field experiment was carried out on a slightly undulating postglacial moraine landscape with a soil developed on noncalcareous moraine. Solum had a duplex arrangement (very fine sandy loam above sandy clay loam); the transition boundary varied as a result of natural processes. The introduced crop rotation was: potato - spring wheat - spring barley. Three separate fields as treatments (without organic manure; straw + mineral nitrogen; cattle manure) were compared within the range of five mineral nitrogen doses. The plots were arranged into field blocks: longitudinal strips with organic manure crossing with nitrogen rates. Each treatment had three replicates (plots), and the longest distance between the plots compared was 80 m. The potato field received straw from succeeding spring barley in the amount of 4 Mg ha⁻¹ and farmyard manure at a rate of 60 Mg ha⁻¹, ploughed under in October. The experimental plots have received similar treatments since the experiment was established. During the first rotation, all plots were P and K fertilised to maintain moderate fertility levels. Two mineral-N fertilisation levels were selected for this study: non-fertilised (N0) and NH₄NO₃. (8 g N m⁻² y⁻¹, i.e. 80 kg ha⁻¹). Repeated spring deep chisel harrowing was applied to the potato field in order to improve the structural and thermal properties of the soil – this is the usual practice in Estonia. Potatoes were planted in furrows 70 cm wide, with rows 20 cm apart. Repeated inter-row tillage was applied until the flowering. Spring barley was sown in rows situated 12.5 cm apart, 550 plants per quadratmetre. The plot size was 5 x 10 m. The sandy soils cropped with spring barley

were fertilised with mineral nitrogen (8 g m⁻²). The soil types and topsoil characteristics are presented in Table 1.

Sampling

The soil was sampled with a steel cylinder (4 cm in diameter). Four subsamples were taken from each plot and joined into one composite sample (200 cm³) for animal extraction. In the case of vertical distribution studies, topsoil was divided into two sampling layers: from 0–5 cm up to 5–10 cm. As the activity of *Collembola* in the surface layer depends on the soil-surface temperature, a stable sampling time interval between 10...12 o'clock was kept. In the barley field, soil cores were taken from the inter-rows; in the potato field, on the half height of furrows. In comparative studies, the sampling for different crop or soil texture was carried out on the same dates and from the same sampling locations.

Collembola estimation

Modified Mcfayden's (1962) extractors were normally run for 4 days and water was used as the collection medium. Soil cores were placed loosely on 2-mm screens. The extracted organisms were examined under a binocular microscope. The *Collembola* were identified to the genus level and, if possible, to the species level. The structural classification proposed by Gisin (1943), who divided collembolans into three groups according to their principal ecological niche in soil: atmobiotic (epedaphic), hemiedaphic and euedaphic, was used.

Statistical analysis

A multifactorial design was applied for IOSDV field trial, with the year (1999 and 2000), crop species (barley and potato) and fertilisation (with and without) as the factors. Soil texture (sandy loam and sand) or depth (0–5 cm and 5–10 cm) were analysed in paired (*t*-test) way.

RESULTS AND DISCUSSION

The dominant species accounted for approximately 80–90% of the *Collembola* collected within each treatment (Table 2). A few representatives of *Sminthuridae* and *Poduridae* were found. In general, the species composition was similar for different crops and years. A large number of *Collembola* emerged as juveniles in September, which generally caused a rise in population peaks. The soil was covered with crop only for four months of each year and regular ploughing turned crop residues deep into the soil, which had an adverse effect on surface *Collembola*. As it was expected in regularly ploughed soil, the euedaphic *Collembola* were the dominant ecological group during the cropping season as conditions were more stable deeper below the ground.

Table 2. Collembolan genera/species dominantly found in the experiment.

Ecological group	Genus	Species
Hemiedaphic	Isotomidae	<i>Isotoma notabilis</i>
		<i>Folsomia fimetaria</i>
	Entomobryidae	<i>Lepidocyrtus cyaneus</i>
Euedaphic	Onychiuridae	<i>Mesaphorura krausbaueri</i>
		<i>Onychiurus armatus</i>

The quantities of Collembola during the growing season in the 0–5 cm soil layer under potato are shown in Fig. 2. The quantity of euedaphic Collembolans in the potato field varied from 140 up to 6,350 individuals per square metre, whereas hemiedaphic species were several times less numerous (Fig. 3). Unfortunately, to the author’s knowledge, there are no reported data on Collembola in cropped soils in the Baltic region, however, the overall mean density is similar to agricultural soils in temperate climate conditions.

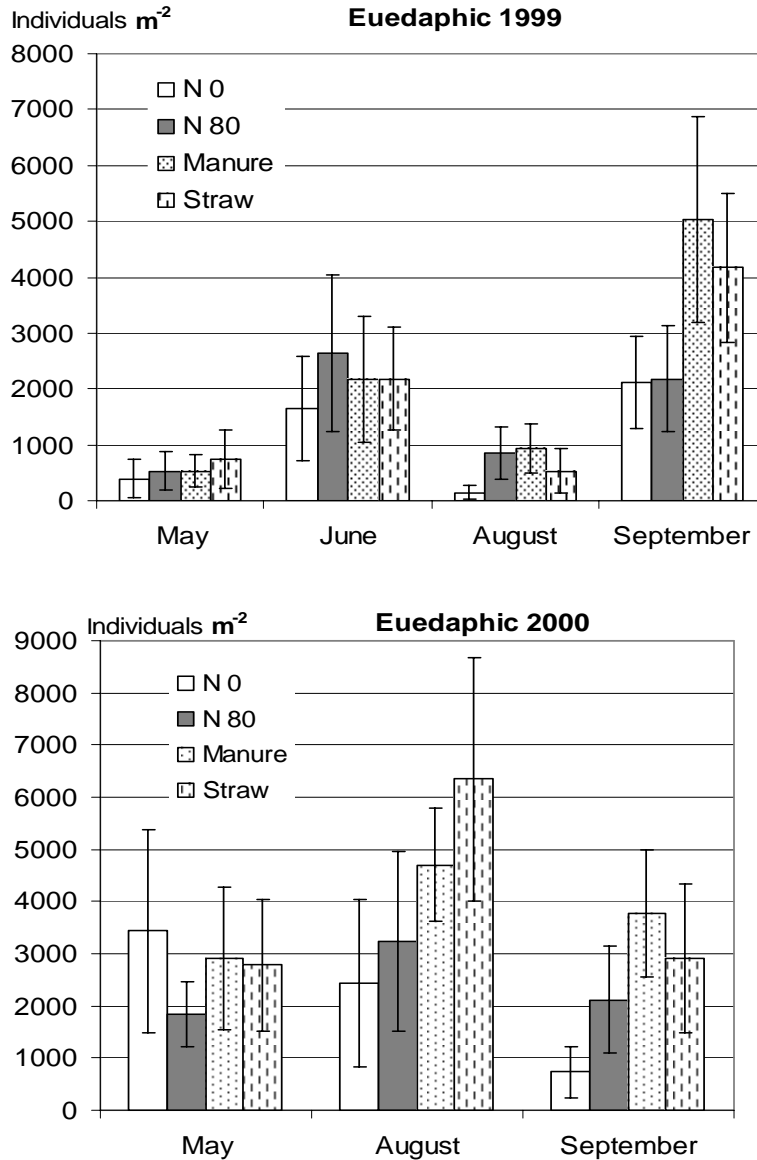


Fig. 2. Mean abundances of euedaphic Collembolan under different fertilisation in the potato field in 1999–2000. Each value is the mean of three replicates \pm standard error.

There was also considerable but not drastic variation in chemical topsoil parameters between the treatments and sites (Table 1 & 3). Considering the duration of the field experiment and the frequency and amount of manure application, fluctuations were expected to occur in habitat conditions due to periodical return of organic residues. During autumnal ploughing, organic amendments and crop residues were buried down up to 250 mm, but the intensive chiseling during seedbed preparation in spring lifted them up, to some extent. However, during the growing season, the density of euedaphic Collembola was not significantly dependent on the treatment. Averaged across treatments, Collembola density was greater in fertilised than in unfertilised soil.

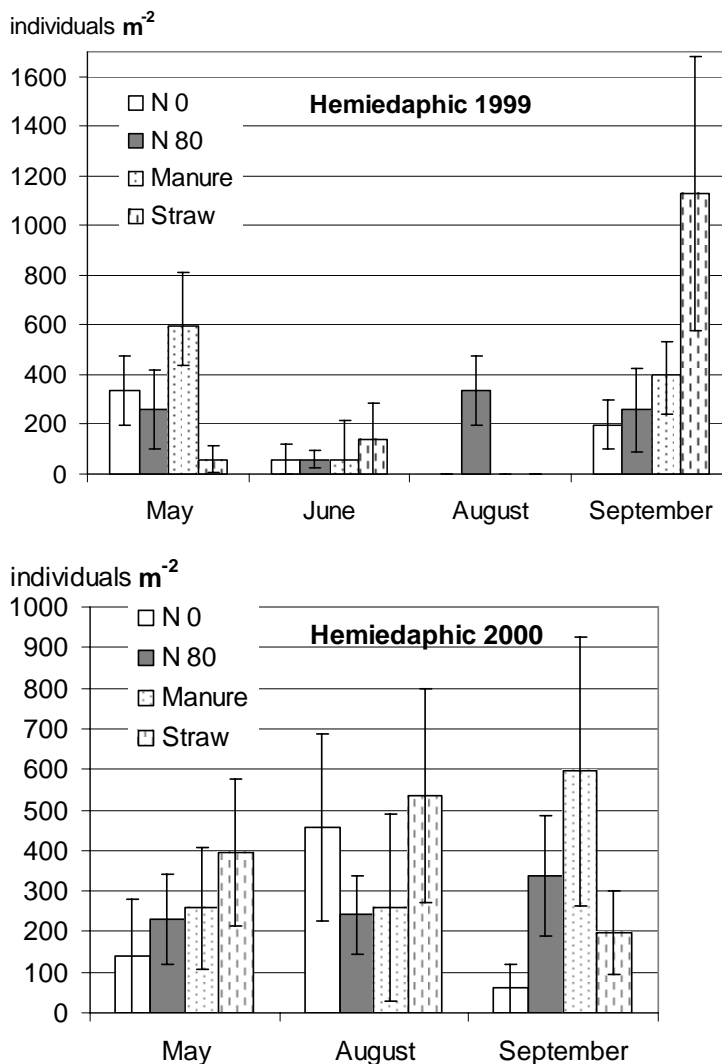


Fig. 3. Mean abundances of hemiedaphic Collembolan under different fertilisation in the potato field in 1999–2000. Each value is the mean of three replicates \pm standard error.

The sole significant difference between manured and unmanured soil was found at the end of the growing season in 1999. Nevertheless, recordings from both years indicated that in unfertilised (N0) soil the average quantities of Collembola remained lower than in organically manured plots. Our investigation showed that in slightly acid field soil with low humus content, the variation coefficient of Collembola population was high. There was little consistent evidence of the enhancing effect of organic matter on Collembola densities, despite significant differences in soil pH values and C content between manured and unfertilised treatments (Table 3).

Table 3. Chemical soil parameters of the investigated potato field (the average plots).

Treatment	pH _(KCl)			Corg g kg ⁻¹		
	1999	2000	mean	1999	2000	mean
N 0	6.36	5.84	6.10 a*	9.7	9.6	9.65 b
N 80	6.11	5.63	5.87 ab	10.4	9.5	9.95 ab
Manure + N80	5.83	5.69	5.76 ab	11.0	10.8	10.90 a
Straw + N80	5.54	5.62	5.58 b	9.9	9.9	9.90 ab
LSD ₀₅	0.35			1.1		

a*: values followed by the same letter are not significantly different ($P < 0.05$)

Seasonal change in the abundance

The peak time of Collembola density appeared to vary depending on the climatic conditions. The influence of rainfall was more pronounced than the influence of temperature. In May and August 2000, monthly rainfall was twice as high as that recorded in 1999 (Fig. 1); the population size of euedaphic Collembola showed a similar, i.e., increasing, shape (Fig. 2). In July 2000, rainfall amount was twice as high as the long-term average. In these conditions Collembola sampling succeeded for spring barley, but failed for potato, because sampling had to be carried out during continuous rain and an insufficient number of individuals were extracted from the very wet surface soil layer of 5 cm. In September the population sizes were similar for both years, although weather conditions in 1999 were milder than in the comparatively colder and drier year of 2000. The improved food supply from crop residues was probably a more decisive factor than weather conditions as soils can hold temperature at the level required for the survival of Collembola. Surprisingly, the proportion of hemiedaphic species in 1999 was higher in May and also in September (Fig. 3), when the soil was covered sparsely with plants or with stubble and the surface temperature fluctuated highly on a daily basis. One possible explanation is that in relatively bare soil conditions hemiedaphic species hide themselves deeper between soil particles than during the period when the soil is densely covered by crop. The declines in population in the middle of the growing season in 1999 can be related to the drought in July (Fig. 1).

Effect of soil texture

Microarthropods live in air-filled soil pores and therefore depend on the soil macrostructure; they are hygrophilous organisms. The soils under examination were of different texture class, but the physical properties of the soils were not so different as initially expected (Table 1). The low humus contents of both soils and soil compaction

caused by machinery were the main reasons. Two different soil layers were simultaneously studied: the uppermost 0–5 cm and the following 5–10 cm.

Significant differences in euedaphic Collembola numbers were found in the uppermost soil layer during the first sampling in May (Fig. 4). It could be attributable to chance, but it may also be a seasonal effect as sandy soils warm up quicker and this enhances the overall biological activity in spring. The quantity of hemiedaphic species showed non-indicative fluctuations (data not shown). Thus, in regularly ploughed fields the Collembola community was, during the growing season, evenly distributed within the uppermost 10 cm of light textured soils. However, the rainy summer of 2000, without the typical topsoil drying in the middle of the growing season, may have additionally contributed to the uniform distribution of Collembola.

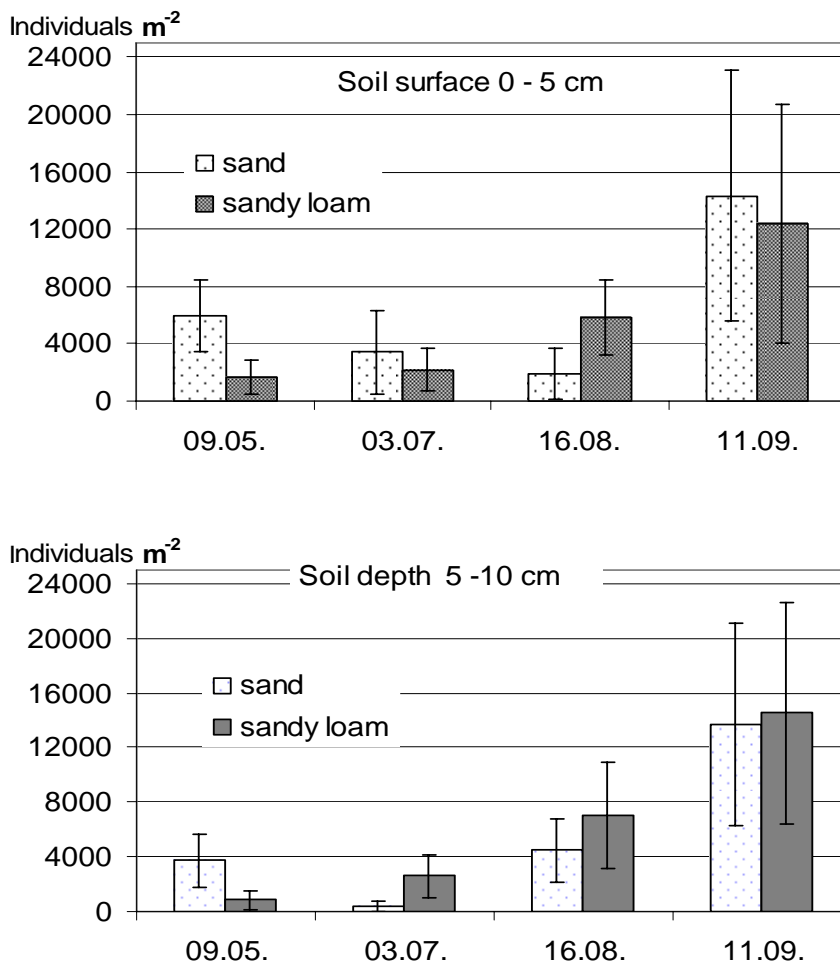


Fig. 4. Depth distribution of a total collembolan community in different soil textures under spring barley (2000). Each value is the mean of three replicates \pm standard error.

Effect of crop cover on Collembola

For comparing the effect of different crops in crop rotation, where crops rotated in space and time, researchers have to assume that the soil environment under different crops was similar. During the moist growing season in 2000, the Collembola population showed continuous growth (Fig. 5). No significant crop effect was found on the density of Collembola until September, when harvested spring barley plots showed four times higher quantities of euedaphic Collembola than estimated under potato. Apparently, the stubble field contributed to an ecologically more favourable living habitat for Collembola than the potato field with its sparse senescent haulms.

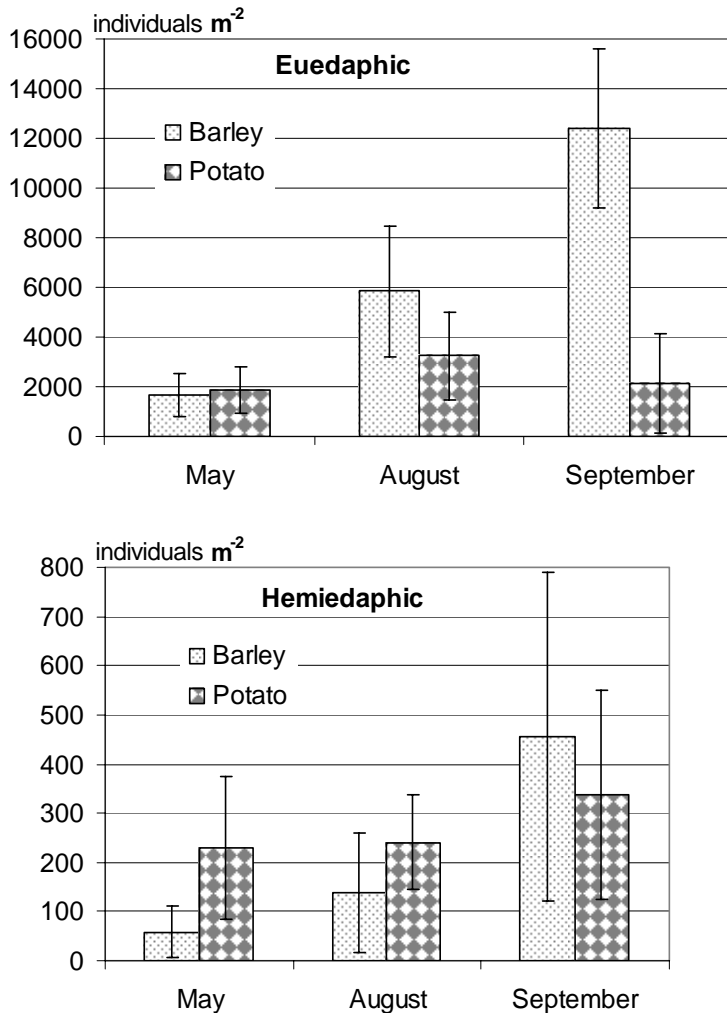


Fig. 5. Mean number of collembolan groups under the same fertilisation treatment (N_{80}) but under different crop (2000). Each value is the mean of three replicates \pm standard error.

To explain the changes of Collembola abundance during the transition from spring cereal to potato, additional sampling was carried out under spring barley in August 1999. August was selected for comparison, because the soil was physically stabilised from tillage by then and both crops covered similar soil surfaces. Fig. 6 shows that the population of euedaphic Collembola under spring barley was affected by mineral fertilisation. After an annual interval it appeared that the population had increased on low-density plots and decreased on high-density plots, despite decade-long differences in crop residue return or favourable moisture conditions in 2000 (Fig. 1). It was hypothesised that the euedaphic community was subjected to density dependent regulation to achieve the optimum population size that a given soil conditions can support despite significant year-to-year changes towards the end of the growing season.

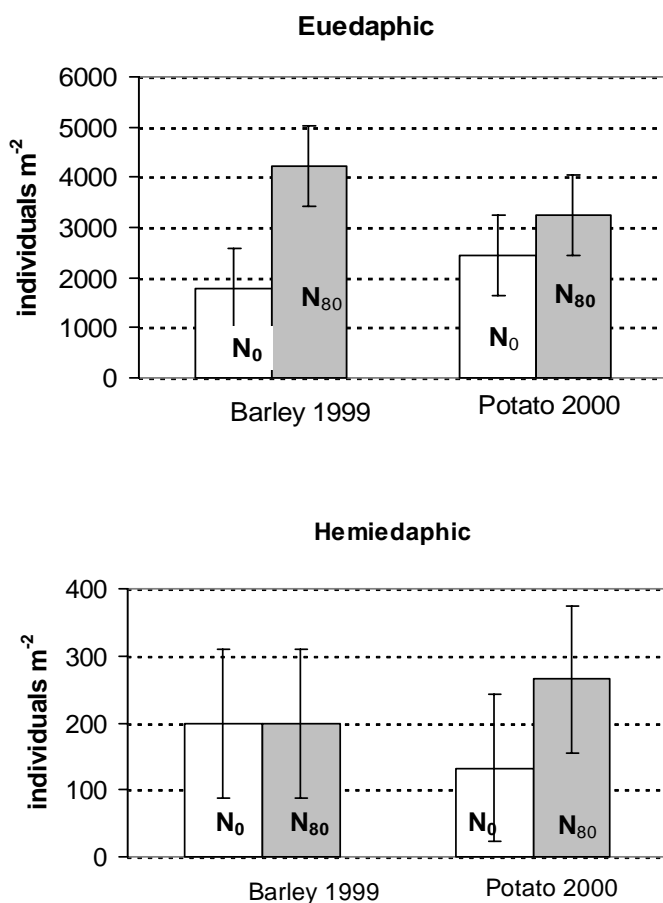


Fig. 6. Density of a collembolan community in soil a year after the shift from spring barley to potato. Each value is the mean of three replicates \pm standard deviation.

In the studied arable soils, the abundance of Collembola was low: only five dominant species were identified. This is symptomatic of cultivated soils in many countries and especially of soils with destroyed microstructure (Rusek, 1998). Collembola generally show idiosyncratic associations with agronomic disturbance as the relative response to different treatments varies, depending on the year (Wardle et al., 1999). In our experiment there were several abiotic pre-requisites, such as the low organic matter content and the weak structure of the soil and annually different weather conditions, to establish the positive effect of different long-term fertilisation patterns on the density of Collembola. Organic manure has chemically and structurally different properties; fresh material is generally more rewarding nutritionally than dead plant material. High densities of Collembola under green manure treatment have been measured on light soils (Filser, 1995; Axelsen & Kristensen, 2000), also in comparison with farmyard manure (Zillingen-Geilen, 1992). Perhaps straw and partly decomposed farmyard manure are less attractive for Collembola directly as a food base than indirectly as they lead to an increase in the populations of cellolytic bacteria and fungi in the soil, which has been observed in response of straw application (Eitminavičiute et al., 1976; Kanal et al., 1999).

In laboratory experiments a connection has been established between straw, fungi and the quantity of *Folsomida candida* in soil (Leonard and Andersen, 1991). Although autumnal manure application and the following ploughing may diminish the direct value of organic manure for the uppermost plough layer, the cumulative effects from previous applications remain. The presence of buried straw loosens the soil above plough depth and increases soil pore continuity in the long term (Ball et al., 1990), which might plausibly enhance the quantity of Collembola in a weakly structured soil. In the soil compaction experiment with straw amendment, the mean number of *Folsomia fimetaria* was 10 to 30 times higher when compared to no amended series, but the abundance declined significantly with increasing bulk density from 1.21 g cm⁻³ (Larsen et al, 2004). The bulk densities measured on our fields are remarkably higher (Table 1). Numerous studies have shown that the application of organic manure or its combination with mineral fertiliser induces higher density of Collembola than measured on unmanured soil (Artemjeva & Gatilova, 1975; Lagerlöf & Andren, 1991; Butz-Strazny, 1996; Bandyopadhyaya et al., 2002; Culik et al, 2002), but similarly to our study, most of these reported differences remain insignificant. Generally manured plots show larger quantities, but also the largest fluctuations, especially at the end of the growing season. Regular ploughing homogenised the overall chemical and physical properties of the soil, but uneven distribution of organic residues within the plough layer was reported earlier (Kanal & Kölli, 1996). Perhaps, closer examination of spatial food resource portioning could clarify the sporadic appearance of Collembola in field soils.

Technical factors

Numerous factors contribute to the inconsistent results, but perhaps the two biggest obstacles to overcome are temporal and spatial variability. Temporal variability can be induced by variability in climatic conditions that affect soil temperature and cause inconsistent treatment responses. The abundance of Collembola varies considerably within the growing season, but variations between treatments were often lower than variations between triplicate plots (replications). Among the soil parameters

studied, we did not find any explanation for the higher population density on some particular plot (microsite) and the overall uneven distribution pattern in the field, except for the aggregated way of living, characteristic of Collembola. Hemiedaphic species showed sporadic distributions during the study, but they are relatively mobile and therefore capable of escaping during the soil coring procedure. The sampling technique had less influence on the measurement of euedaphic Collembola, whose moving ability is severely limited: for *Onychirus armatus* just 1–2 cm per day has been reported (Bengtsson et al., 2002). Hemiedaphic Collembola, who lives near the surface, is also more vulnerable to mechanical disturbance; ploughing may lower the population of Isotomidae (Petersen, 2002).

Sampling a larger area could increase the spatial heterogeneity in the data set as some Collembola species have restricted spatial distributions within arable fields (Frampton, 2000). It is possible that the spatial resolution of sampled plots was too coarse for the local soil heterogeneity and therefore masked the fertilisation effect. In our study, the longest distance between plots was 80 m, which is a relatively small scale for actual management practice in farms. The influence of spatial effects needs further research; however, spatial variability reflects, to some extent, also uneven distribution of biotic conditions in soil; e.g. Joosse (1971) supposed that Collembola live in an aggregated manner, because of a favourable habitat, food supply and reproduction.

Soil as a dynamic environment

A serious problem for soil-related ecological research is posed by the fact that abiotic and biotic properties of soil change simultaneously and continuously during the growing season and especially under annual cropping schemes. On one side, plough layer becomes denser during cropping season but, on the other side, roots make it looser (Kanal & Vipper, 1994). The indirect effect of aboveground vegetation and increases and decreases in root activity during the growing season change the physical, chemical and biological soil environment. Small-scale studies have demonstrated that microbial and microfaunal activity is concentrated on spatially discrete and heterogeneously distributed sites (“hotspots”), which are enriched with organic substrates (Griffiths, 1994). Roots and organic residues in soil form these microsites in the plough layer, but these locations alter in space and time. For both annual crops under examination, it was found that Collembola populations increase towards autumn. The post-harvest residues remained not only on the soil surface, but also in the soil. The decomposition of dead barley roots has been shown to give a much greater microfaunal population than in the rhizosphere of living plants (Christensen et al., 1992). Significant treatment-related differences in the amount of Collembola were established not in the middle, but at the beginning or at the end of the growing season (Fig. 4 & 5), when few living roots met in the soil. Presumably, the expansion of living roots into soil rearranges the habitat and makes the food web less dependent on the limited food base originating from crop residues of the previous year. If organic residues are closely related to fertilisation and manure application, recent root remains production is relatively independent of the nutrient level (Merckx et al., 1987). Probably an expanded root system diminishes discrepancies between differently fertilised plots during the growing season.

Edaphic properties

Among the chemical parameters of soil, the most pronounced effect on Collembola might be expected from pH (Hågvar & Abrahamsen, 1980) and from the content of organic carbon (Kovač & Miklisová, 1997). The natural fertility of the soil under examination was comparatively low (Table 1). The main influencing factors – organic carbon (Corg) and pH, remained also within relatively narrow limits. Our results agree with those reported by Kovač et al. (2001): approximately under similar soil properties (Corg *ca* 2%, pH_{H₂O} *ca* 6.0, clay loam), no correlation was established between the mean quantities and the diversity of Collembola and the values of pH and Corg in cropped soil. Perhaps, the influence of soil chemical properties on Collembolan communities is limited and, in Humic Gleysol, moisture content and organic carbon content explains only 33% of the variation of Onychiuridae and Entomobryidae on clay loam soil under continuous corn (Fox et al., 1999). However, if we compare taxonomically different soils, even a 8% higher clay content and a 0.5% higher organic carbon content caused the occurrence of larger quantities of Collembola in Eutric Fluvisol than in Albic Luvisol (Kovač & Miklisová, 1997). In maple forests of the temperate climate zone, the distribution of endogeic species within organic and organo-mineral horizons was clearly related to mull or moder humus type (Chagnon et al., 2000). In a German oak-hornbeam and spruce forest, in which repeated liming and fertilisation changed considerably soil parameters, no change was detected in Collembolan community composition over time (Geissen & Kampichler, 2004). Consequently, more drastic differences were needed in the edaphic properties of compared soils than it was achieved with the soil management procedure applied in our field experiment (Table 1 & 3).

Collembola with their restricted burrowing ability depend on a macropore system in soil. They tend to avoid narrow pores, probably in order to protect their wax coat against damage (Choudhuri, 1961). For example, in Fluvic Cambisol with clay texture and at least twice as large organic matter content as in the case of our study, no euedaphic species were found in topsoil (Gardi et al., 2002). Sandy soil has usually higher macroporosity and lower water storage capacity than soil with a heavier texture. In earlier studies – before the exploitation of heavy machinery for soil tillage – sandy soils have been shown to have remarkably high levels of Collembola density compared to loam (Müller & Rauhe, 1959). In the case of our study, soil moisture was not limited in 2000 (Fig. 1) and, despite differences in texture (very fine sandy loam versus sand), both soils showed similar abundance (Fig. 4). Both soils in this experiment can be considered to have a deteriorated structure and, therefore, under similar crop the habitable pore space for Collembola remained similar (Table 1).

Crops

Quick establishment of healthy and dense crop cover is possible by effective application of mineral fertilisers and manures, which ensures not only proper yield, but also higher return of crop residues into soil. For soil organisms it means improvement in habitat and food supply. In the long term, it should change the quality of topsoil. The beneficial effects of additional crop residues produced after mineral fertilisation in barley did not appear for Collembola in the relative fertile Mollic Gleysol (Lagerlöf & Andren, 1991). With Podzoluvisols with weaker chemical and physical properties, mineral fertilisers increase the amount of crop residues and spring barley produces

twice as much as potato (Kanal & Kõlli, 1996), thus, by selecting an appropriate crop sequence, it is possible to regulate the quantity of Collembola. Closer examination of the spatial distribution of food resources could clarify the sporadic appearance of Collembola in field soils. For instance, it appeared that the effect of compaction on abundance was most pronounced when the food base was relatively large (Larsen et al, 2004).

Generally, monocropping systems might have a more direct influence on the quantity, and probably also the diversity, of Collembola, owing to longer adaptation time with a particular crop than it is possible in the case of crop rotation. In crop rotation, the population density seemed to be held on an average level determined by the general properties of the soil.

CONCLUSIONS

In our ten-year-old field experiment, we could not detect any systematic change of collembolan community composition as a consequence of fertilisation. Cyclic changes in the abundance of collembolan communities have been observed with an increase towards autumn. The results of this study show that critical assessment is required over the choice of Collembola as bioindicators of fertilisation type.

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