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ABSTRACT

Movement of soil microarthropods associated to searching or foraging behaviour has received scanty attention and remained largely unexplored. However, rare studies on soil Collembola suggested that their exploratory behaviour is an important feature of population dynamics. In the current study based on a microcosm experiment we tested the influence of food sources tied to a distant patch on the foraging behaviour of springtails. The microcosms consisted of five separate 5 cm sections bound together. Only the last part of the microcosms (section 5) differentiated the 3 treatments with no food (C), microflora (M) or microflora + plant (M+P). Collembola were introduced into the first section. The mean covered distance of total collembolan differed between all the treatments. It continuously increased from 0.9 (± 0.3) cm in C through 4.7 (± 1.0) cm in M to 7.4 (± 1.2) cm within M+P. Concomitantly, the mean covered distance was also influenced by the factor “life-form” with on average 7.3 cm covered by the epedaphic species which was 73.8% more than hemiedaphic and 82.5% more than euedaphic. Even if differences between life-forms were detected, our results also revealed differences of exploratory pattern between species belonging to the same life-form. Our study clearly shows that springtails are reactive to the quality of their environment, in particular food sources.

Keywords : Movement, Life-forms, Collembola, Microcosm

1. INTRODUCTION

Studying the movement *sensu lato* of organisms is a key topic in ecology (Dieckmann et al., 1999; Levin et al., 2003). Processes like migration, dispersal or foraging influence the dynamics of populations, the distribution and abundance of species and therefore the community structure. Migration is furthermore known to be involved in speciation processes and in the evolution of life-history traits (Winker, 2000). Consequently movements of organisms affect ecosystem functioning by modifying living assemblages and the nature and strength of biotic relationships. One main reason that forces organisms to move, explore or disperse is foraging. For example, animals can be attracted by the odour of their food (Auclerc et al., 2010; Salmon and Ponge, 2001). They may also be forced to move owing to overcrowding or antagonism from competing species (Ronce, 2007).

Many data and models of foraging, dispersal or migration are now available for many organisms (Nathan, 2001). However, with the exception of a few groups like ants (Lenoir, 2003) or soil living-herbivores (Schallhart et al., 2011), movement associated to searching or foraging behaviour within the soil has received scanty attention and remained largely unexplored (Hassall et al., 2006; Mathieu et al., 2010). However, rare studies on soil animals suggested that their searching and foraging behaviour is an important feature of population dynamics (Bengtsson et al., 1994a; Bengtsson et al., 2002b; MacMillan et al., 2009).

Collembola constitute a dominant, well investigated and diverse soil microarthropod group. Many studies have proven the direct or indirect contribution of Collembola to belowground functioning such as N mineralisation, soil respiration or leaching of dissolved organic carbon (Filser, 2002). Many indirect effects of Collembola on soil processes operate through interactions with the microflora. Several studies higlighted that Collembola critically depend on food sources provided by the soil microflora (Hopkin, 1997).

63 Gisin (1943) described three typical soil collembolan life-forms based on morphology and
64 habitat. Briefly, epedaphic species are usually large bodied species, have a high metabolic
65 activity, consume a food substrate of a high quality and are surface-dwellers. Conversely,
66 euedaphic species are deep-living species that consume low-quality food and have a low
67 metabolic activity. Euedaphic species are small-sized, colorless with reduced appendices
68 (e.g. furca, antennae, leg). Finally, the hemiedaphic group includes species sharing
69 intermediate attributes (Petersen, 2002; Rusek, 1989). Collembolan assemblages are thus
70 well-structured on a vertical spatial scale matching the resources dispatched by plants either
71 above- (litterfall) or belowground (roots and root exudates).
72 While several studies focused on the dispersal of springtails (Auclerc et al., 2009;
73 Bengtsson et al., 2002a; Ojala and Huhta, 2001), few focused on foraging (Bengtsson and
74 Rundgren, 1988; Bengtsson et al., 1994b; Hagvar, 2000). According to the fact that dispersal
75 capacity relates beside other factors to locomotor activity, comparatively large epedaphic
76 springtails with good jumping skills and well-developed legs should be more efficient
77 foragers than euedaphic species. However, species with directional sense perception may
78 also have a high probability to forage successfully (Mitchell, 1970).
79 In the current study based on a microcosm experiment we thus wanted to test the
80 influence of two food sources tied to a distant patch on the foraging behaviour of springtails.
81

2. MATERIAL & METHODS

2.1 Microcosm setup

2.1.1 Substrate

The substrate used was sourced from a deciduous forest (*Fagus sylvatica*) located within the Campus of the University of Rouen. The soil was an endogleyic dystric Luvisol (FAO) developed on more than 80 cm of loess (lamellated siltloam) lying on clay with flints. The humus form is a dysmoder. The C:N ratio of the A horizon was of about 15.3 and the pH H_2O 3.9. We collected on a square meter the F and H organic horizons of the topsoil. Once in the laboratory, one part of the organic substrate collected was used in the microcosms and another part served to collect the Collembola to be introduced within them as explained below.

The microcosms, adapted from a previous experiment on nematodes (MacMillan et al., 2009), were made of 5 plastic tubes arranged in a row-like configuration (total length 25 cm, diameter 5 cm). Each plastic tube corresponds to a section (numbered 1 to 5) bound together with adhesive tape, and sealed at each end with a plastic cap to prevent escape of animals (Fig. 1). For all tests, the organic substrate filling the compartments 1 to 5 of the microcosms was first sterilized by autoclaving at 105°C with two successive cycles of 1h separated by 24h, then was sieved at 5 mm and carefully mixed before filling the different sections.

Only the last part of the microcosms (section 5) differentiated the treatments:

- In the “microflora bio-assay”, abbreviated M in the following text, the sterilised organic substrate dedicated to section 5 was reinoculated with soil microflora. A suspension of soil microflora was obtained after shaking 500 g of fresh organic

substrate with 2.5 L of distilled water during 1h. The suspension was then filtered in two successive steps: first at 250 µm and then using filters for qualitative microbial analysis (DURIEUX n°149). Ten millilitres of this suspension were transferred into each section 5. This was repeated three times waiting 12h between each inoculate. The same amount of distilled water was added to the other sections.

- In the “microflora+plant bio-assay”, abbreviated M+P in the following text, one week after reinoculation of microflora, a plant (*Hyacinthoides non-scripta* (L.) Chouard ex Rothm., 1944) was added to section 5. Plants of the same morphology, around 10 cm tall, were collected in the forest, their roots were washed with distilled water and slightly cut to homogenise their morphology.
- In the “control bio-assay”, abbreviated C in the following text, no further treatment was applied to the substrate of the section 5 compared to compartments 1 to 4. In each section of the control bio-essay, ten millimetres of distilled water was added three times as it was done in the two previous bio-assays.

The tubes used for the sections 5 were also pierced (1.5 cm in diameter) on top to allow introduction of the microflora suspension and the plants. Whatever the treatments, the section 5 was separated from section 4 with a fine-mesh (20 µm) plastic gauze to minimize or exclude propagation of soil biota (microflora and roots) to adjacent compartments. In each microcosm one centimetre was left empty between the substrate and the top of the tubes to allow movement of surface dwelling collembolans. Four replicate microcosms were used per treatment.

2.1.2 Introduction of Collembola

From the non-sterilised part of the organic substrate collected, Collembola were extracted alive using the dry funnel method above trays filled with moist clay as collectors and then were transferred using a pooter to sections 1 through a hole (1.2 cm diameter) pierced on top of the tubes. After springtails were introduced, the hole was closed with a plastic plug caps. The amount of substrate used for extracting Collembola corresponded to the amount of substrate used to fill in the sections 1 plus 50% to obviate for mortality during the transfer into the microcosms. Because it is known that death odour is repellent for Collembola (Nilsson and Bengtsson, 2004), a two-week period was left before introducing them into the microcosms.

The microcosms were incubated at room temperature for 12 days. We selected this time lapse because to the light of preliminary experiments 12-day was judged enough to allow migration but not reproduction to occur. However, we cannot rule out that some deposition and hatching of eggs deposited in the meantime by fertile females probably occurred, thereby increasing the error but not the treatment effect. The sections were then carefully separated and the collembolans were recovered from them by the dry-funnel method, counted and determined at species level following several keys (Gisin, 1960; Hopkin, 2007). The soil water content in the different microcosms was determined by drying 5 g of soil at 105 °C for 48 h (Alef and Nannipieri, 1995). Furthermore, at the end of the experiment, the microbial C biomass (Cmic) of sections 5 was determined by means of the fumigation-extraction method (Jenkinson and Powlson, 1976). Before and after fumigation, 20 g of fresh soil was shaken for 1 h in a solution of K2SO4 at 0.05 M then filtered at 0.45 µm and analysed for dissolved organic C on a Shimadzu-TOC-L series.

2.2 Data Analysis

153 For each treatment, we determined the exploratory behaviour of each species, then of
154 each life-form and finally of the whole assemblage, using the following calculation:
155 Exploratory behaviour = (n2 + n3 + n4) / N * 100
156 Where ni = number of individuals recovered in section i, and N = total number of individuals
157 within the microcosm.
158 In parallel we also evaluated the Collembola movement according to the following formula:
159 Mean covered distance = p1*d1 + p2*d2 + p3*d3 + p4*d4
160 Where pi = proportion of individuals in section i from the total recovered in sections 1-4, and
161 di = distance from the application point to the centre of section i.
162 For each level of observation (assemblage, life-form and species of Collembola) the
163 impact of the factor "Treatment" upon the exploratory behaviour and the mean covered
164 distance was tested by means of General Linear Models (GLM). GLM with single categorical
165 predictor can be called a one-way Anova design. The same test was applied for the microbial
166 C biomass and the soil water content.
167 For each treatment, differences between the percentages of Collembola recovered within
168 each section were tested by GLM with Section as fixed factor. Prior to analyses, percentage
169 data were arcsin transformed. In all cases, significant differences between means were
170 tested at the 5% level using the Tukey HSD test. All statistical analyses were performed with
171 the STATISTICA® software package (version 7.0, Statsoft®, Tulsa, OK).
172

3. RESULTS

The microbial C biomass differed between the treatments ($F = 38.1$, $p < 0.0001$) with on average almost 18 times more Cmic in the M+P treatment than in the Control and twice more than in the M treatment (Fig. 2). In opposite, no difference of soil water content could be established between the treatments ($F = 0.907$, $p = 0.44$) with an overall mean (± SD) of 53.2 (± 2.6) % of dry weight.

There were no significant differences between the treatments regarding the total amount of springtails recovered from the microcosms ($F = 2.25$, $p = 0.16$) with an overall mean (± SD) of 76.1 (± 15.4) individuals per microcosm.

3.1 Collembolan Assemblages

The mean (± SD) exploratory behaviour in the control bio-assay (C) was of 15.3% (± 5.3) and increased to 62.0% (± 11.5) in the microflora treatment (M) and to 78.7% (± 5.6) in the microflora+plant treatment (M+P).

The mean covered distance of total collembolan differed between all the treatments ($F = 50.37$, $p < 0.001$). It continuously increased from 0.9 (± 0.3) cm in C through 4.7 (± 1.0) cm in M to 7.4 (± 1.2) cm within M+P.

The amount of collembolan found in the different sections differed in the C and the M treatment ($F = 302.6$, $p < 0.001$ and $F = 11.8$, $p < 0.001$, respectively). In C, only less than 3% of the springtails moved beyond the section 2 (Fig. 3A). When adding microflora in the fifth separated section, a maximum of individuals was found in section 2 (about 40% of the total amount). Still in M, the percentage of collembolans recovered in sections 1 and 2 did not differ but both were significantly higher than in sections 3 and 4. A total of 25% of the

196 collembolans were found in these two last sections (Fig. 3B). In M+P, a similar percentage of
197 individuals was recovered in all sections ($F = 3.1$, $p > 0.05$; Fig. 3C).
198
199 **3.2 Life-forms**
200 The factor “life-form” had a significant effect on the exploratory behaviour ($F = 13.83$; $p <$
201 0.001). Epedaphic collembolans had an overall exploratory behaviour of 76.2% significantly
202 higher than both hemiedaphic and euedaphic, with similar values of 56.5% and 48.4%,
203 respectively.
204 The different life-forms showed a similar pattern of exploratory behaviour across the
205 treatments. Each life-form had similar values in both M and M+P, being twice higher for
206 epedaphic and 5 to 6 times higher for hemiedaphic and euedaphic than in C (Table 1).
207 Concomitantly, the mean covered distance was also influenced by the factor “life-form” ($F =$
208 22.2, $p < 0.001$) with on average 7.3 cm covered by the epedaphic which was 73.8% more
209 than for hemiedaphic and 82.5% more than euedaphic. The mean distance covered by the
210 epedaphic was almost twice higher in M and M+P than in C (Fig. 4). The same pattern was
211 obtained for the euedaphic springtails with 7.1 (± 0.8) cm covered in M+P and only 0.6 (±
212 0.2) cm covered in C. Finally the distance covered by the hemiedaphic was different for each
213 bio-assay ranging from 0.9 (± 0.3) cm in C to 7.6 (± 1.7) cm in M+P. While strong differences
214 existed in the mean distance covered between the life-forms in the C and M treatments,
215 these differences disappeared in M+P (Fig. 4).
216
217 **3.3 Species-level**
218 Four different groups of species could be distinguished according to their exploratory
219 response to the treatments (Table 2). Group 1 was made of species showing a foraging

pattern (mean covered distance) that did not differ between the treatments: *Mesaphorura macrochaeta* and *Friesea truncata*. On average (± SD), species of this group covered a distance of 4.2 (± 2.7) cm. *Lepidocyrtus lanuginosus*, *Entomobrya multifasciata*, *Sminthurinus signatus*, and *Folsomia quadrioculata* belong to a second group with a mean distance covered significantly modified by the addition of food resources but without differences between M and M+P treatments. In the control treatment, members of this group covered on average (± SD) a distance of 2.3 (± 1.0) cm, while in M and M+P considered together they covered a mean (± SD) distance of 7.8 (± 1.1) cm. The group 3 was only made of *Protaphorura armata* which was only affected by the M+P treatment. While in C and M considered together, *P. armata* covered a mean (± SD) distance of 0.9 (± 1.8) cm, the addition of a plant (M+P) increased its movement to reach an average (± SD) distance of 7.9 (± 3.2) cm. Finally the fourth group was made of species showing significantly different mean distances covered for each treatment: *Isotomiella minor* and *Parisotoma notabilis*.

4. DISCUSSION

Movements of animals can be considered over a wide range of spatial and temporal scales. In large-scale movements they migrate in response to a deteriorating habitat, optimum breeding conditions or physiological signals, basically independent of resource limitation. Passive dispersal has been also advocated to explain large-scale dispersal of collembolans (Hawes, 2008). Small-scale movements, covering only a small part of a population, are often due to local resource limitations (e.g. space or food) and may be triggered by feeding activities or by intraspecific antagonisms (Bowler and Benton, 2005; Bullock et al., 2002; Clobert et al., 2001). Our study clearly demonstrates the importance of foraging behaviour, based on distant patch quality recognition, for the movement of

collembolans. The absence of food at a distant point leads to almost no exploratory behaviour of springtails. However, enriching the last part of our devices with a food item had a significant effect on the distribution of Collembola. Collembolans are known to move towards sources of CO_2, which they locate in a similar way as plant parasitic nematodes find CO_2-emitting roots in soil (Klinger, 1965). This may explain the higher dispersal distance covered by Collembola when a plant was introduced in the distant section. Furthermore, the higher microbial C biomass in the M+P treatment may also, through a higher amount of volatile compounds, be responsible for the higher attraction of springtails. The highest mean dispersal distance estimated in our study (4.3 cm/week) is in the range of values reported previously in forest soil (Ojala and Huhta, 2001). This may indicate that our design did not cause a strong bias in springtails behaviour, at least at the community level.

According to morphological traits of collembolan life-forms, a positive gradient of efficient dispersal is often observed from euedaphic to epedaphic species (Ojala and Huhta, 2001). This is only partly supported by our data. Epedaphic species had the highest mean dispersal distance whatever the treatment, but no difference was found between the mean dispersal distance of euedaphic and hemiedaphic species in the different treatments. Apparently, as stated by Sjögren (1997), jumping abilities of springtails species do not fully correlate to their dispersal rates. Interestingly, however, the exploratory behaviour of epedaphic species was weakly impacted by the different treatments while the addition of different food resources strongly modified the patterns of both hemi- and euedaphic species. Mechanisms responsible for migration of epedaphic species might differ from those in play for the two other life-forms. Epedaphic species, living in a fluctuating environment in opposite to hemi or euedaphic, are rather considered as r species. Such strategists are often good dispersers and pioneer species with therefore an exploratory behaviour not necessarily

directed toward a more favourable habitat. However our design, specifically the humified substrate used, offered rather unnatural conditions to epedaphic species compared to hemi and euedaphic species. This may have affected their behaviour and consequently their movement. It is thus difficult to conclude if we underestimated the distance they could covered due to the disadvantage of the substrate or if we overestimated it because they wanted to get away from this unnatural condition. Our results regarding this life-form might thus be interpreted with caution.

Even if differences between life-forms were detected, our results also revealed differences of exploratory pattern between species classified into the same life-form. For example, half of the euedaphic species had a similar average distance of dispersal between the three treatments while the other half showed strong differences of distance covered between the treatments. This supports the view of several authors (Hågvar, 1983; Sjögren, 1997) concluding that morphologically equal species can show very different dispersal rates. Feeding behaviour may be an important point in this respect. Through a stable isotope approach, three feeding guilds in springtails were distinguished not correlated to life-forms (Chahartaghi et al., 2005): phycophages/herbivores, primary decomposers and secondary decomposers. According to data given by these authors, our four groups do not correspond to the food habits revealed by δ15N signatures, because our group 2 (migration affected by food resources) was made of both primary and secondary decomposers. This can be explained by the fact that in our experiment species with longer legs and furcula moved over longer distances, which was also shared by species strongly attracted to microbes and/or roots. Although our design was not purposed to demonstrate it, our results point to a behavioural trade-off between dispersal rate and attraction to food resources.

291 The distance covered by *Protaphorura armata*, one of the few euedaphic species to be
292 phytophagous (Hopkin, 1997), was highest when a plant was introduced in a distant patch.
293 Bengtsson et al. 1994a also found *P. armata* to be attracted by mycorrhizal fungi. By
294 contrast, *Friesea truncata* a predatory euedaphic species, covered the same distance
295 whatever the treatment. Although not significant, *F. truncata* showed a slight tendency to
296 cover a higher distance in the microflora and plant treatment. It is probable that this species
297 feeding on eggs of collembolan (Hopkin 1997) started to respond to the overall collembolan
298 movement and that extending the experiment would have reinforced this process.
299 Nevertheless besides feeding behaviour, size should also be considered. For example,
300 *Mesaphorura macrochaeta,* though known as fungivorous only showed a tendency to
301 migrate more when a food source was tied at a distant patch. The very small size of *M.*
302 *macrochaeta* (the smallest species of our experiment) and thus its low active mobility might
303 explain this pattern. Finally, differences of pattern between quite similar species in terms of
304 ecology, for example *Parisotoma notabilis* and *Folsomia quadrioculata*, are interesting to
305 notice, because rather unexpected. However, Ojala et al. 2001 also found that *F.*
306 *quadrioculata* covers lower distance, by 34%, than *P. notabilis* in field conditions. Biotic
307 interactions (intra or interspecific) may also surely play a role. Bengtsson et al. 2002
308 documented a positive relationship between conspecific density and migration pattern of a
309 soil collembolan. Our study was not design to test for this specific factor, but it may have
310 played a role on the observed pattern. Furthermore we cannot exclude the fact that our
311 design favoured or in contrary disadvantaged the movement of several species. For example,
312 it is known that juveniles and adults may have very different behaviour and dispersal
313 patterns (Ronce, 2007).

Despite abovementioned limitations of laboratory experimental designs, which can never reproduce the real environment of soil animal communities, our study revealed that the presence of food (roots and/or microflora) influenced the migration of collembolan species which differ according to the four criteria: morphology, life-form, feeding guild and dispersal rate. We showed that none of them fully explained the active foraging of species placed at distance from a food source, pointing to species-specific response patterns that can only be explained by a combination of several criteria. Awaiting more complete screening, Table 2, although based on a little number of species, can be suggested as a guide for field functional ecologists.

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416
417

418 **Table 1**: Mean exploratory behaviour (in percentage) with standard deviations of
419 collembolan life-forms within three treatments corresponding to different food sources tied
420 to a distant patch. Means of the same life-form sharing identical letters are not significantly
421 different (Tukey HSD test). C: control; M: microflora treatment; M+P: microflora and plant
422 treatment. Ep: Epedaphic, He: Hemiedaphic, Eu: Euedaphic.

	Treatments		
	C	M	M+P
Epedaphic	45.6^{B} (26.5)	91.1^{A} (6.0)	91.2^{A} (6.8)
Hemiedaphic	17.2^{B} (5.8)	66.4^{A} (21.2)	86.0^{A} (7.9)
Euedaphic	11.3^{B} (4.4)	58.9^{A} (6.9)	74.9^{A} (5.0)

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Table 2: Mean covered distance (in cm) with standard deviations of different collembolan species covered after 12 days within three treatments corresponding to different food sources tied to a distant patch. Species are grouped according to their response pattern. Means of the same species sharing identical letters are not significantly different (Tukey HSD test; P level of significance: n.s. = not significant; ** = < 0.01; *** = < 0.001). C: control; M: microflora treatment; M+P: microflora and plant treatment. Ep: Epedaphic, He: Hemiedaphic, Eu: Euedaphic.

Group	Species	Life-form	F	P	C	M	M+P
1	*Mesaphorura macrochaeta*	Eu	3.2	n.s.	2.0^{A} (1.0)	5.4^{A} (3.4)	6.0^{A} (2.2)
	Friesea truncata	Eu	4.2	n.s.	1.1^{A} (1.3)	5.2^{A} (2.7)	4.2^{A} (2.0)
2	*Lepidocyrtus Lanuginosus*	Ep	8.9	**	5.7^{B} (2.3)	11.2^{A} (1.0)	10.6^{A} (2.5)
	Entomobrya multifasciata	Ep	8.3	**	1.9^{B} (2.2)	7.2^{A} (1.6)	6.9^{A} (2.4)
	Folsomia quadrioculata	He	66.0	***	0.6^{B} (0.3)	4.3^{A} (0.8)	4.8^{A} (0.6)
	Sminthurinus signatus	He	22.6	***	0.9^{B} (1.2)	7.8^{A} (2.5)	9.9^{A} (1.9)
3	*Protaphorura armata* gr.	Eu	12.9	**	0.0^{B} (0.0)	1.7^{B} (2.4)	7.9^{A} (3.2)
4	*Isotomiella minor*	Eu	70.1	***	0.8^{C} (0.6)	4.4^{B} (0.9)	9.3^{A} (1.5)
	Parisotoma notabilis	He	92.7	***	0.2^{C} (0.3)	3.8^{B} (0.8)	10.9^{A} (1.7)

Figure 1

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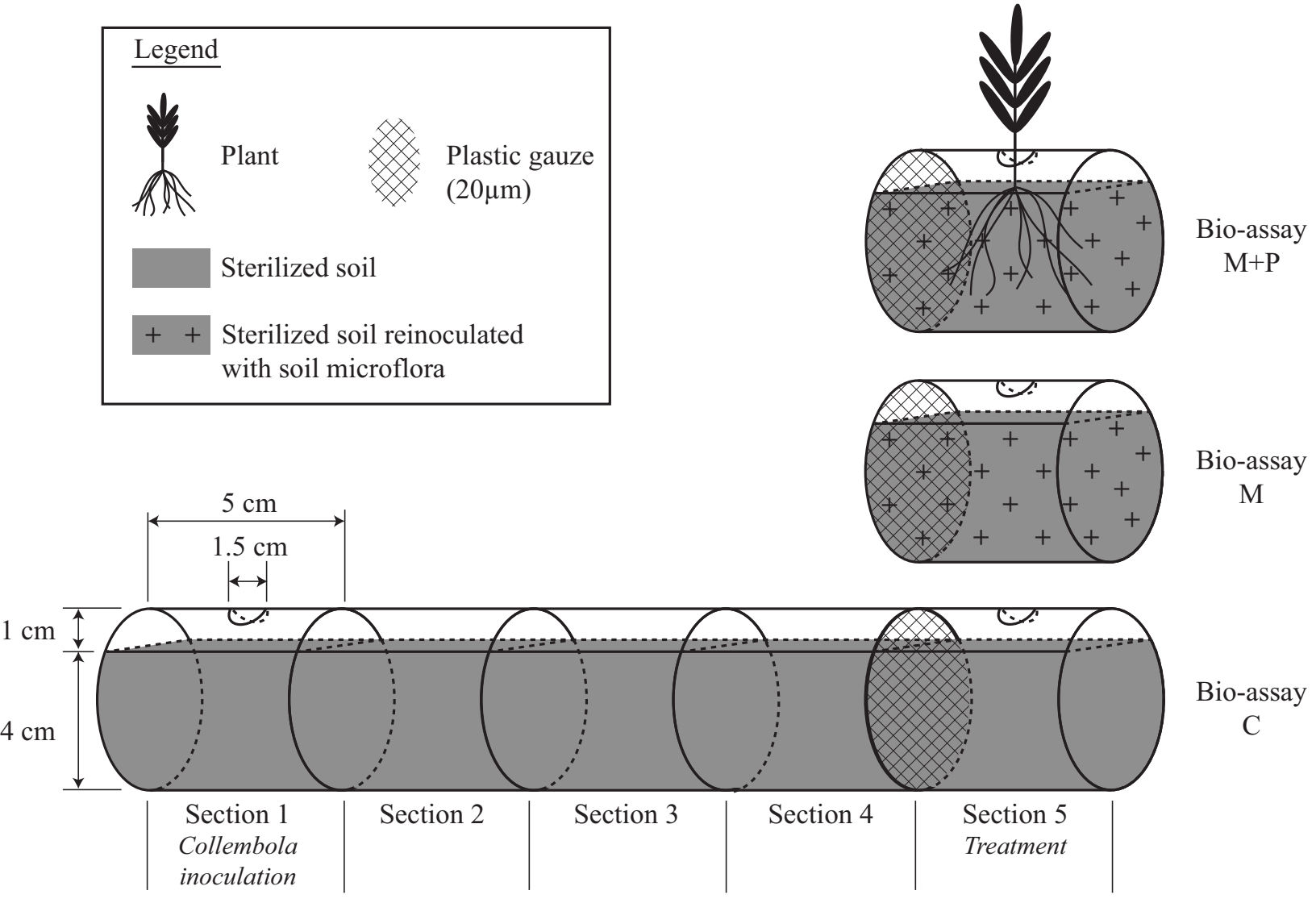

Figure 2

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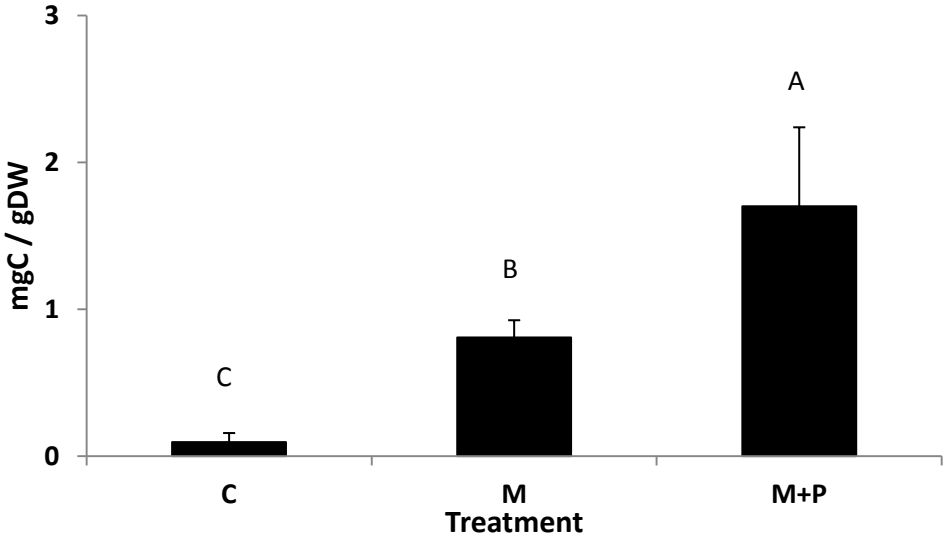

Figure 3

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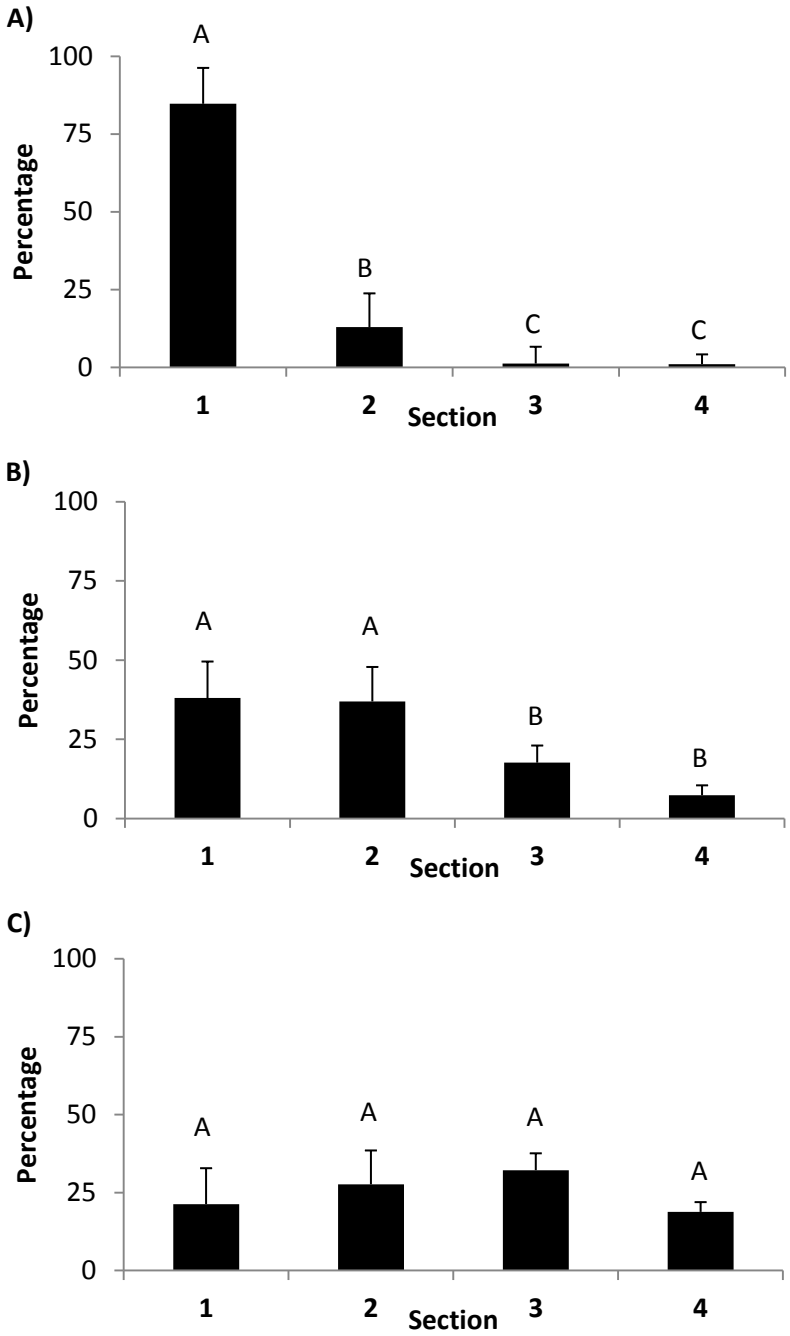

Figure 4

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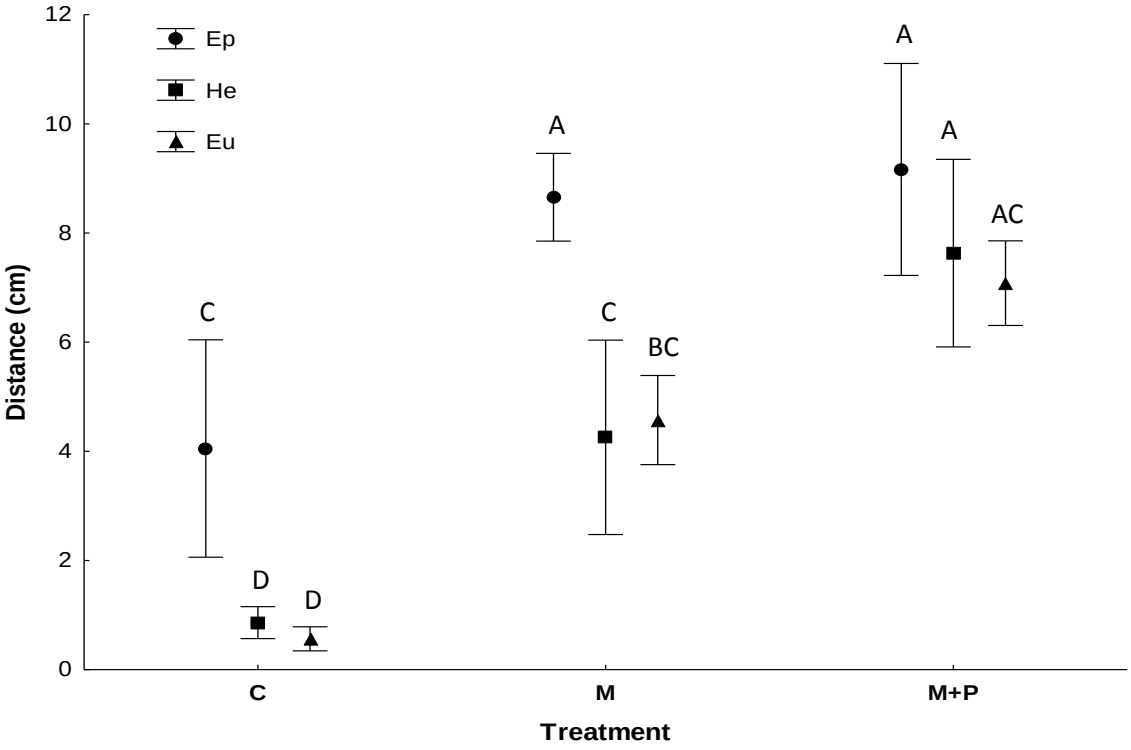

APPENDIX 1

Mean (and SD) number of Collembola found in each section (1 to 4) of the microcosms according to the different food sources placed at a distant point (section 5). C : control bio-assays ; M : microflora bio-assays ; M+ P : microflora and plant bio-assays

Section	C	M	M+P
1	72 (22.2)	26.8 (6.0)	17.8 (3.4)
2	10.3 (2.2)	26.8 (8.7)	23.5 (7.4)
3	1 (0.8)	13 (5.4)	27.3 (5.2)
4	1 (0.8)	5.5 (3.1)	16.3 (8.6)
Total	84.3 (21.7)	72 (9.5)	84.9 (13.2)