Original research article

Relationships among distribution of fine roots, soil DOC concentration and Collembola

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Abstract: The higher abundance of microarthropods around plant roots has been considered to result from the release of labile carbon by roots (*e.g.,* root exudation), but the concentration of labile carbon itself has not been measured. We investigated whether fine root distribution affects distribution of Collembola (*Folsomia candida*) by changing the soil dissolved organic carbon (DOC) concentration, which is supposed to represent rhizodeposits, under both low- and high-light conditions using a sandy soil system with *Chamaecyparis obtusa*. Fine root biomass and total DOC content were greater under the high-light condition than under the low-light condition, but no significant difference was detected in collembolan abundance. In addition, soil DOC concentration was correlated with fine root biomass, but collembolan distribution was not affected by root or DOC distribution under either light condition. Although it remains unsolved why collembolan distribution did not correspond to the fine-root or DOC distribution, our results indicate that there is the case of no significant correlation between roots and Collembola.

Keywords: Collembola, dissolved organic carbon, fine roots, *Folsomia candida*, Japanese cypress (*Chamaecyparis obtusa*), spatial distribution

Abbreviations: DOC, dissolved organic carbon

Introduction

Soil microarthropods are one of the most widespread and abundant groups of arthropods, and play important roles in ecosystem process such as litter decomposition and nutrient cycling in terrestrial ecosystems (Hopkin 1997, Filser 2002). Knowledge about the distribution pattern of soil microarthropods is important for understanding where these ecological functions operate strongly and is helpful in explaining about difference of plant growth in terms of soil nutrient availability. The spatial distribution of soil microarthropods has been explained in terms of various environmental factors including soil water availability, porosity, chemistry, and organic matter content (Verhoef and van Selm 1983, Hågvar and Abrahamsen 1984, Didden 1987, Cassagne et al. 2003, Detsis 2009). Plant root systems, especially fine roots, are also an important factor involved in the distribution of soil microarthropods, because roots generally alter the surrounding environment physically, chemically, or biologically, by penetrating soils, absorbing nutrients, and releasing rhizodeposits (Whalley et al. 2005, Pinton et al. 2007).

To assess the effects of roots on soil microarthropod distribution, several studies have compared the abundance of microarthropods between places with abundant roots and those with few roots, under both field and experimental conditions (Wiggins and Curl 1979, Wiggins et al. 1979, Parmelee et al. 1993, Eo and Nakamoto 2007, Hishi et al. 2008). Most of these studies demonstrated that the abundance of microarthropods was greater in root-abundant places, and it was speculated that the release of labile carbon (*e.g.*, root exudation) by the roots resulted in the

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higher abundance of soil microarthropods (Wiggins et al. 1979, Parmelee et al. 1993, Eo and Nakamoto 2007, Hishi et al. 2008). Recent studies using stable isotope labeling techniques have demonstrated that soil microarthropods such as Collembola utilize root-derived carbon (Ostle et al. 2007, Endlweber et al. 2009), and then, the higher abundance of soil microarthropods around plant roots could possibly result from the release of labile carbon by the roots. However, as far as we know, it is still unknown whether plant root biomass affects the concentration of labile carbon in the soil (*i.e.*, whether plant root distributions produce a concentration gradient of labile carbon), while labile carbon has a high mobility with water and may diffuse readily from the plant roots. Thus, the concentration of labile carbon should also be measured when the distribution of soil microarthropods around plant roots is investigated.

In the present study, we investigated whether root distribution affects distribution of Collembola by altering the concentration of soil dissolved organic carbon (DOC), which is supposed to represent rhizodeposits (*i.e.*, labile carbon). We constructed an autotroph microcosm poor in carbon sources other than plant roots by using sand and red clay soil (akadama soil), because DOC fluxes derived from rhizodeposits are quantitatively low and often undetectable in soils that include other organic materials. We applied high- and low-light conditions in a greenhouse to construct different systems with regard to fine root biomass, distribution, and DOC concentration, because these traits are strongly affected by the light environment (Zagal 1994, Grayston et al. 1996, Reich et al. 1998). We then evaluated the correlations among fine root biomass, DOC concentration, and abundance of Collembola.

Materials and Methods

Experimental set up

The experiment was conducted in a greenhouse at the Kitashirakawa Experimental Station of Kyoto University in Kyoto City (35°02′N, 135°47′E), Japan. The mean temperature throughout the study period was 20.4°C. The temperature in the greenhouse was not manipulated, but light was controlled to create low-light and high-light conditions by shading with black mesh. The light intensity under the low- and high-light conditions was approximately 5 and 25% full sunlight, respectively, based on comparisons with outdoor photosynthetic photon flux density (μmol photons m^{-2} s^{-1}).

In April 2009, first-year seedlings of *Chamaecyparis obtusa* Endl. were transplanted individually into pots (height 18 cm, top diameter 20 cm, bottom diameter 14 cm), which were filled with 3.5 L of soil each. The soil consisted of a sand and akadama soil mixture (2:1). Akadama soil is red clay soil consisting of sub-angular structure of the same size (2-6 mm in diameter), which is originated from the loamy layer of the Kanto Region, central Japan, with a small quantity of carbon (about 1.41 %). The soil was autoclaved at 120°C for 2 h for defaunation and sterilization. The reinoculation of microorganisms and microfauna was conducted as described below. Fresh soil was taken from the forest floor of the natural *C. obtusa* forest at the Kamigamo Experimental Forest Station of Kyoto University, about 12 km north of Kyoto City (35°04′N, 135°43′E) and 100 mL of soil were suspended in 1 L of distilled water for 12 h. The suspension was filtered through 75-μm mesh to exclude mesofauna, and 100 mL of this soil suspension were added to the soil of each pot. After the inoculation with microorganisms and microfauna, approximately 1000 individuals of the euedaphic Collembola species, *Folsomia candida*, were added to each pot. *F. candida* has been used as a model organism for the tests for response to many environmental factors (Fountain and Hopkin 2005) and is considered to have a close relationship with rhizodeposits as a carbon source because of its enhanced growth with the application of glucose (Kaneda and Kaneko 2004). The individuals used in the present study were isolated from the laboratory colony at Yokohama National University and cultured with dry yeast in an incubator at 20°C in the dark; the generation time of these individuals were about 20 days. Three replicates were prepared for each light condition. To avoid direct effects of the different light intensities, soil surfaces were covered with porous shading sheets. However the soil temperature was affected by light manipulation: the mean soil temperature was 0.8°C higher under high-light condition than under low-light condition. Plants were watered with 30 mL every other day, which is determined to avoid drain from the bottom of the pots and keep soils moist. Plants were fed every 40 days (four times during experimental period) with 20 mL of nutrient solution (5 mM KNO_3, 1 mM $NH_4H_2PO_4$, 2 mM $Ca(NO_3)_2 \cdot 4H_2O$, 5 mM $MgSO_4 \cdot 7H_2O$). The concentration of nutrient solution was adjusted to the values lower than the annual nutrient fluxes at a site of relatively low nutrient availability in a Japanese temperate forest (e.g., approximately 20 kg N ha^{-1} $year^{-1}$: Tokuchi et al. 1999). The pots were set on workbenches, which were about 50 cm above the ground, in order to avoid contamination of other collembolan species. Although all pots were contaminated mainly by soil surface-dwelling Sminthuridae spp (on average, 30 individuals per pot), only *F. candida* (on average, 60 individuals per pot) was

used for analysis.

Measurements

After seven months (in November 2009), to allow time for the proliferation of several generation of *F. candida*, the plants were harvested and the soil was sampled. A shoot was cut off from each pot, dried at 40°C to constant mass, and then weighed. The soil in the pot was divided into 12 subsamples by cutting the horizontal plane into quarters and cutting the vertical plane into three equal parts by thickness (top, middle, bottom). The abundance of Collembola, fine root biomass, DOC concentration, and water content of each subsample were measured. Collembola in each soil subsample were extracted using a Tullgren funnel at 35°C for 5 days and counted under a stereomicroscope. After the extraction of Collembola, fine roots (≤ 1.0 mm in diameter) were separated from the soil and weighed, and then the soil dry weight was measured. Fresh soil for measurements of DOC concentration and water content was taken before collembolan extraction. Each 5-g fresh soil sample was extracted with 25 mL deionized water by shaking for 1 h and then the suspension was filtered through a 0.45-μm PTFE membrane filter (Advantec, Tokyo, Japan). The dissolved C content of the suspension was determined by measuring NPOC (Non-purgeable Organic Carbon) using a total organic carbon analyzer (TOC-V carbon analyzer, Shimadzu, Kyoto, Japan). Each fresh soil (approximately 2-3 g) was weighed and oven-dried at 105 °C for 48 hours to determine its water content. The water content of each soil subsample was calculated using the following formula: water content = (fresh weight of soil – dry weight of soil) / dry weight of soil (g g^{-1}).

Statistical analysis

The mean values of plant biomass, total DOC content in a pot, water content calculated by using all soil subsamples in a pot, and total abundance of Collembola in a pot were compared between the high- and low-light conditions using *t*-tests (n = 3). Pearson correlation coefficients were used to analyze the relation among the abundance of Collembola, fine root biomass, DOC concentration, and water content per subsample. Two-way nested analysis of variance (Two-way nested ANOVA) with pot nested was used to assess the effects of the vertical position in a pot (top, middle, bottom) and light condition on the abundance of Collembola, fine root biomass, DOC concentration, and water content per subsample. Because the division of soil subsamples was conducted freehand and the weight of subsamples differed individually, the abundance of Collembola and fine root biomass were determined by the amount in a subsample divided by the weight of the subsample soil, as follows: $Y = X_s / W_s$, where X_s represents the contents in a subsample, and W_s is the weight of the subsample soil (kg). The values of Collembola and plant biomass were log-transformed in *t*-tests and Two-way nested ANOVA. Statistical analyses were performd using R 2.14.1.

Results

Plant biomass and total DOC content were significantly greater under the high-light condition than under the low-light condition (Table 1). On the other hand, water content and collembolan abundance were higher under the low-light condition, but these differences were not significant.

The DOC concentration was positively correlated with fine-root biomass under both high- and low-light conditions (Fig. 1A). The abundance of Collembola showed no significant correlation with fine root biomass and DOC concentration under either the high- or low-light conditions (Fig. 1D, E). Water content has a positive effect on the abundance of Collembola under the high-light condition in this study, but it was not statistically significant (Fig. 1F: high-light; $P = 0.074$, low-light; $P = 0.234$).

Table 2 shows the effects of light condition and vertical position on collembolan abundance, fine root biomass, DOC concentration and water content. Fine root biomass was affected by light condition, while water content was affected by position in the pot and was higher at lower position in both light conditions (Table 2 and Table 3). There were no significant interaction between effects of light and position for all variables.

Table 1. Plant biomass, total dissolved organic carbon (DOC) content, and total abundance of Collembola in pots under high- and low-light conditions

	High-light	Low-light
Leaves (g)	1.84 (0.01)[a]	1.06 (0.09)[b]
Stem (g)	0.43 (0.02)[a]	0.23 (0.03)[b]
Total roots (g)	0.85 (0.08)[a]	0.38 (0.03)[b]
Fine roots (g)	0.52 (0.09)[a]	0.23 (0.04)[b]
DOC (mgC pot^{-1})	4.54 (0.21)[a]	3.80 (0.15)[b]
Water content (g g^{-1})	0.26 (0.03)[a]	0.30 (0.01)[a]
Collembola (ind. pot^{-1})	47.33 (20.02)[a]	78.00 (14.73)[a]

Means (SE) followed by different letters are significantly different (*t*-test, $p < 0.05$).

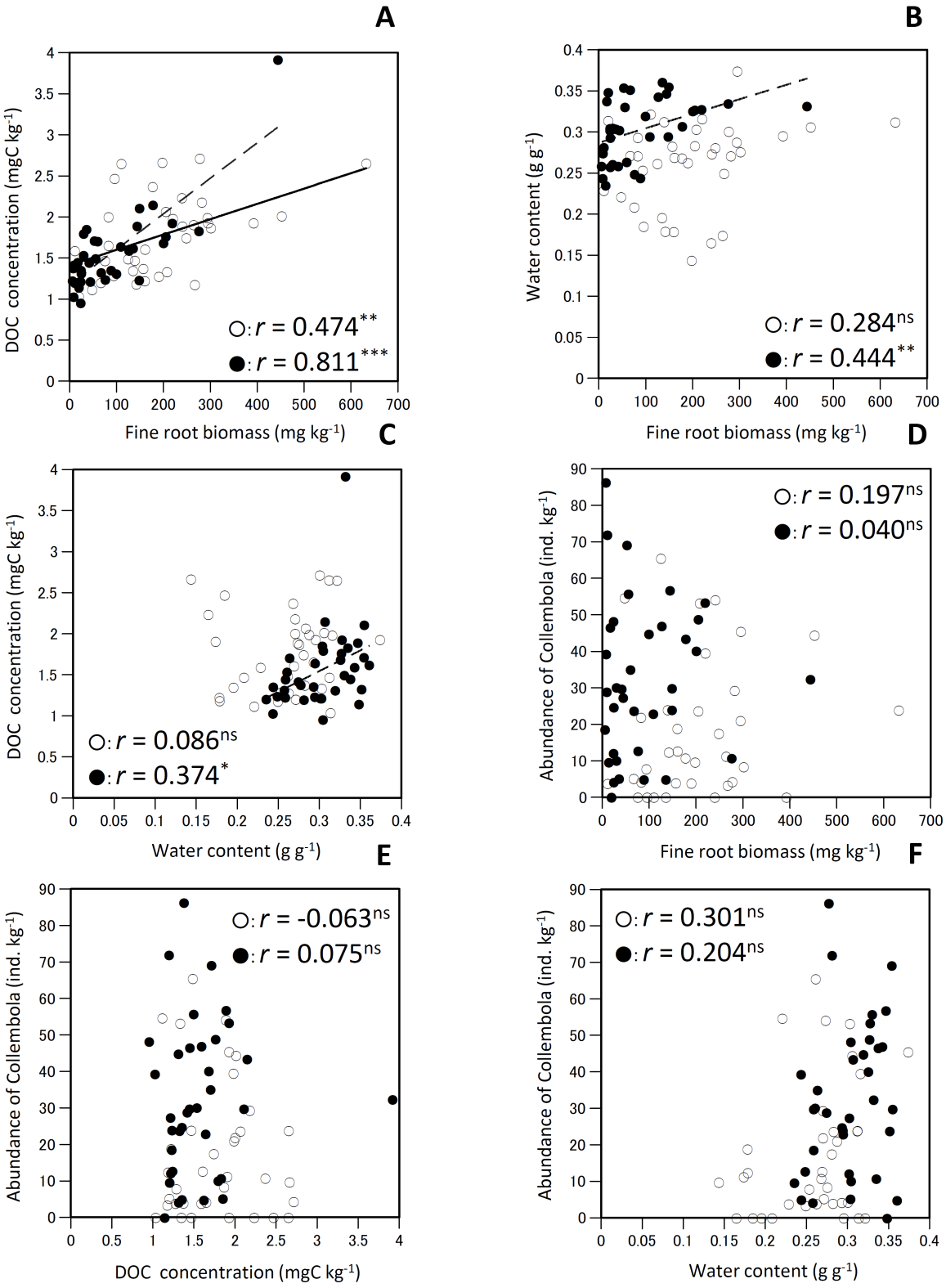

Fig. 1. Relationships among collembolan abundance, fine root biomass, dissolved organic carbon (DOC) concentration, and water content under high-light (open circle) and low-light (black circle) conditions. Values of Pearson correlation coefficients are indicated in each graph. Asterisks indicate statistical significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, ns not significant. Significant relationships are represented by solid line (high-light condition) or dashed line (low-light condition).

Table 2. Mean (SE) of abundance of Collembola, biomass of fine roots, dissolved organic carbon (DOC) concentration, and water content of subsamples from three pots in each position (top, middle, bottom) in the pots under high- and low-light conditions (n = 3)

light condition	Positon in pot	Abundance of Collembol (ind. kg^{-1})	Fine root biomass ($mg\ kg^{-1}$)	DOC concentration ($mgC\ kg^{-1}$)	Water content ($g\ g^{-1}$)
high-light	top	15.48 (8.79)	176.17 (27.22)	1.68 (0.12)	0.241 (0.033)
	middle	18.90 (12.77)	225.97 (59.69)	1.88 (0.04)	0.258 (0.040)
	bottom	18.81 (6.28)	189.56 (25.77)	1.78 (0.18)	0.283 (0.016)
low-light	top	29.71 (8.79)	50.67 (7.63)	1.37 (0.05)	0.270 (0.012)
	middle	33.56 (3.44)	80.61 (24.50)	1.52 (0.05)	0.301 (0.007)
	bottom	32.90 (9.21)	136.76 (35.58)	1.80 (0.25)	0.338 (0.004)

The abundance of Collembola and fine root biomass were showed by the amount in a subsample divided by the weight of the subsample soil, as follows: $Y = X_s / W_s$, where X_s represents the contents in a subsample, and W_s is the weight of the subsample soil (kg).

Discussion

We aimed to construct different systems by the light environment, and indeed root biomass and DOC content were different between the high versus low light condition. The difference in DOC content between the two conditions is considered to be the result of different carbon productivity caused by the different light intensities. This finding is supported by previous studies, which showed that root exudation was higher under conditions of greater light intensity (Rovira 1959, Zagal 1994, Hodge et al. 1997). The correlation between fine root biomass and DOC concentration under both light conditions means the strong influence of root distribution on the DOC distribution. The DOC distribution was not significantly affected by the vertical position and the DOC concentration corresponded to different fine-root vertical distributions under each light condition: both of the fine root biomass and DOC concentration were highest in the middle position under the high-light condition, and in the bottom position under the low-light condition. Therefore, the influence of fine roots on DOC is considered to be stronger than the influence of the vertical position in the pot, which could affect the DOC distribution due to the high mobility of DOC with water. Khalid et al. (2007) showed that the presence of a plant increases the size of the soil DOC pool in comparison to unplanted soil; furthermore, our study suggests that the DOC concentration was higher in subsamples where abundant fine roots were distributed and the heterogeneity of DOC concentration in the soil was caused by the fine root distribution. However, there were no significant interactions between the effects of light and position, and differences in vertical distribution of fine roots and DOC between both light conditions were not successfully constructed.

Table 3. Nested analysis of variance of position in the pots and light condition for abundance of Collembola, fine root biomass, dissolved organic carbon (DOC) concentration, and water content

	DF	*F*	*P*
Abundance of Collembola (ind. kg^{-1})			
Light	1	2.039	0.227
Position	2	0.003	0.997
Interaction	2	0.516	0.599
Error	62		
Fine root biomass ($mg\ kg^{-1}$)			
Light	1	13.550	0.021
Position	2	2.111	0.130
Interaction	2	2.055	0.137
Error	62		
DOC concentration ($mgC\ kg^{-1}$)			
Light	1	3.807	0.123
Position	2	1.844	0.167
Interaction	2	1.016	0.368
Error	62		
Water content ($g\ g^{-1}$)			
Light	1	1.975	0.233
Position	2	27.579	< 0.001
Interaction	2	1.516	0.228
Error	62		

In this experiment, the abundance of Collembola showed no significant correlation with fine root

biomass and DOC concentration under either the high- or low-light conditions, although many previous studies have shown that microarthropod abundances were higher around plant roots than in the bulk soil (Wiggins et al. 1979, Parmelee et al. 1993, Eo and Nakamoto 2007). In the present experiment, water content and position in the pot, which are other factors involved in collembolan distribution, also did not affect the distribution of Collembola. No significant correlation with roots and DOC may be due to the effects of other carbon sources that were not measured, such as microbial biomass (or respiration as their activity) including mycorrhiza. Root-derived carbon is rapidly used by soil microorganisms after or before exudation and measuring only DOC may not have been enough for the indicator of collembolan food resources. In addition, DOC, which is often measured to quantify rhizodeposits (e.g., Cheng et al. 1996, Khalid et al. 2007), may not have functioned as an appropriate indicator of resource for soil organisms. DOC includes soluble phenolics, which could operate as repellent for soil organisms, other than sugars or amino acids (Qualls et al. 1991; Hishi et al. 2004), and Collembola may have been negatively affected by these compounds.

The relationships between roots and microarthropods were known to be affected by soil substrates. Previous studies found a strong correlation between roots and microarthropods in the mineral soil with little organic carbon, though the correlation was not found in organic layer (Parmelee et al. 1993; Hishi et al. 2008). Although this study used mineral soil containing little carbon in order to detect low DOC concentration released by fine roots, significant correlation between roots and microarthropods was not detected. Whereas previous studies were conducted in the field (Wiggins et al. 1979, Eo and Nakamoto 2007) or used field-collected soils in experimental studies (Parmelee et al. 1993), this study used artificial sand and akadama soil containing little nutrients as well as carbon, and nutrients were supplied by low-concentration nutrient solution. The soil which was low in nutrients may also have caused the no significant correlation between roots and Collembola by nutrient limits for Collembola rather than carbon limits. Compared to the inorganic nitrogen content of field soils (g g^{-1} soil), which has range from 4.30 (Kamigamo Experimental Forest of Kyoto University, Kyoto, Japan) to 31.7 (Field Museum Kusaki of Tokyo University of Agriculture and Technology, Gunma, Japan) (Shibata et al. 2011), soil inorganic nitrogen content (g g^{-1} soil) in the present study was indeed low (high-light: 3.63, low-light: 6.70) by the data obtained in August 2009 from other pots not including Collembola, which were cultivated under the same condition with the pots for this experiments. The growth of soil organisms depending on root-derived carbon in the rhizosphere is known to be limited strongly by nutrients, because roots alter the chemistry of the rhizosphere by absorbing nutrients as well as by secreting carbohydrates (Chapin et al. 2002). In the present experimental condition, soil microbial biomass (mg kg^{-1} soil) in the pots, in which inorganic nitrogen was measured, was very low (high-light: 0.12, low-light: 0.17), and competition for nutrients between roots versus soil organisms could occur in the rhizosphere.

In the current study, soil DOC concentration was correlated with fine root biomass, but collembolan distribution was not affected by root or DOC distribution under either light condition. Further experiments are needed to explain why collembolan distribution did not correspond to the fine-root or DOC distribution in our experimental system. Investigating detailed collembolan carbon resources such as DOC composition or microorganisms and assessing the effects of soil nutrient condition on the relationships between Collembola and plant roots will bring further advances in elucidation of spatial distribution of soil microarthropods.

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References

Cassagne N, Gers C, Gauquelin T 2003 Relationships between Collembola, soil chemistry and humus types in forest stands (France). Biol. Fertil. Soils 37: 355-361.

Chapin FS, Matson PA, Mooney HA 2002 Principles of Terrestrial Ecosystem Ecology. Springer-Verlag, USA, pp. 1-436.

Cheng W, Zhang Q, Coleman DC, Carroll CR, Hoffman CA 1996 Is available carbon limiting microbial respiration in the rhizosphere? Soil Biol. Biochem. 28: 1283-1288.

Detsis V 2009 Relationships of some environmental variables to the aggregation patterns of soil microarthropod populations in forests. Eur. J. Soil Biol. 45: 409-416.

Didden WAM 1987 Reactions of *Onychiurus fimatus* (Collembole) to loose and compact soil: Methods and first results. Pedobiologia 30: 93-100.

Endlweber K, Ruess L, Scheu S 2009 Collembola switch diet in presence of plant roots thereby functioning as

herbivores. Soil Biol. Biochem. 41: 1151-1154.
Eo J, Nakamoto T 2007 Evaluation of root effects on soil organisms under different fertilization regimes by comparing rhizosphere and interrow soil in a wheat field. Plant Root 1: 3-9.
Filser J 2002 The role of Collembola in carbon and nitrogen cycling in soil. Pedobiologia 46: 234-245.
Fountain MT, Hopkin ST 2005 *Folsomia candida* (Collembola): a "standard" soil arthropod. Annu. Rev. Entomol. 50: 201-222.
Grayston SJ, Vaughan D, Jones D 1996 Rhizosphere carbon flow in trees, in comparison with annual plants: the importance of root exudation and its impact on microbial activity and nutrient availability. Appl. Soil Ecol. 5: 29-56.
Hågvar S, Abrahamsen G 1984 Collembola in Norwegian coniferous forest soils III. Relations to soil chemistry. Pedobiologia 27: 331-339.
Hishi T, Fujimaki R, McGonigle TP, Takeda H 2008 Relationships among fine roots, fungal hyphae and soil microarthropods among different soil microhabitats in a temperate coniferous forest of *Chamaecyparis obtusa*. Eur. J. Soil Biol. 44: 473-477.
Hishi T, Hirobe M, Tateno R, Takeda H 2004 Spatial and temporal patterns of water-extractable organic carbon (WEOC) of surface mineral soil in a cool temperate forest ecosystem. Soil Biol. Biochem. 36: 1731-1737.
Hodge A, Paterson E, Thornton B, Millard P, Killham K 1997 Effects of photon flux density on carbon partitioning and rhizosphere carbon flow of *Lolium perenne*. J. Exp. Bot. 48: 1797-1805.
Hopkin SP 1997 Biology of the springtails. Oxford University Press, Oxford, pp. 1-330.
Kaneda S, Kaneko N 2004 Growth of the collembolan *Folsomia candida* Willem in soil supplemented with glucose. Pedobiologia 48: 165-170.
Khalid M, Soleman N, Jones D 2007 Grassland plants affect dissolved organic carbon and nitrogen dynamics in soil. Soil Biol. Biochem. 39: 378-381.
Marschner H 1995 Mineral nutrition of higher plants. Academic Press, London, pp. 1-889.
Ostle N, Briones MJI, Ineson P, Cole L, Staddon P, Sleep D 2007 Isotopic detection of recent photosynthate carbon flow into grassland rhizosphere fauna. Soil Biol. Biochem. 39: 768-777.
Parmelee RW, Ehrenfeld JG, Tate RL 1993 Effects of pine roots on microorganisms, fauna, and nitrogen availability in two soil horizons of a coniferous forest spodosol. Biol. Fertil. Soils 15: 113-119.
Pinton R, Varanini Z, Nannipieri P 2007 The rhizosphere: Biochemistry and organic substances at the soil-plant interface. CRC press, Boca Raton, pp. 1-447.
Qualls RG, Haines BL, Swank WT 1991 Fluxes of dissolved organic nutrients and humic substances in a deciduous forest. Ecology 72, 254-266
Reich PB, Tjoelker MG, Walters MB, Vanderklein DW, Buschena C 1998 Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. Funct. Ecol. 12: 327-338.
Rovira AD 1959 Root excretions in relation to the rhizosphere effect IV. Influence of plant species, age of plant, light, temperature, and calcium nutrition on exudation. Plant Soil 11: 53-64.
Shibata H, Urakawa R, Toda H, Inagaki Y, Tateno R, Koba K, Nakanishi A, Fukuzawa K, Yamasaki A 2011 Changes in nitrogen transformation in forest soil representing the climate gradient of the Japanese archipelago. J. For. Res. 16: 374-385
Tokuchi N, Takeda H, Yoshida K, Iwatsubo G 1999 Topographical variations in a plant-soil system along a slope on Mt. Ryuoh, Japan. Ecol. Res. 14: 361-369.
Verhoef HA, van Selm AJ 1983 Distribution and population dynamics of Collembola in relation to soil moisture. Ecography 6: 387-394.
Whalley WR, Riseley B, Leeds-Harrison PB, Bird NRA, Leech PK, Adderley WP 2005 Structural differences between bulk and rhizosphere soil. Eur. J. Soil Sci. 56: 353-360.
Wiggins EA, Curl EA 1979 Interactions of Collembola and microflora of cotton rhizosphere. Phytopathology 69: 244-249.
Wiggins EA, Curl EA, Harper JD 1979 Effects of soil fertility and cotton rhizosphere on populations of Collembola. Pedobiologia 19: 75-82.
Zagal E 1994 Influence of light intensity on the distribution of carbon and consequent effects on mineralization of soil nitrogen in a barley (*Hordeum vulgare* L.)-soil system. Plant Soil 160: 21-31.