Vertical distribution of Collembola in deciduous forests under mediterranean climatic conditions

Vassilis Detsis

Laboratory of Soils and Agricultural Chemistry, Agricultural University of Athens, Iera Odos 75, 118 55 Athens, Greece

ABSTRACT. This study was conducted in the deciduous forests in the delta of the river Nestos. Soil samples were taken in various seasons and were divided into three layers: O layer, 0-2.5 cm soil depth and 2.5-5 cm soil depth. The Collembola caught were counted and identified and the biomass was determined. Soil moisture and temperature were also recorded.

In most seasons the majority of the animals was found in the O and the upper soil layer. Under adverse conditions in summer (low soil humidity) a vertical migration to deeper layers was observed. No similar response was observed in winter. These patterns persist at the level of the whole Collembola population and at the species level as well. Only minute differences, if any, were observed in the vertical distribution pattern of the most abundant species, irrespectively of the life form they belong to. Generally a preference of smaller animals for the deeper layers was observed.

KEY WORDS: Collembola, vertical distribution, life forms, body size.

INTRODUCTION

A number of studies state that the majority of Collembola live in the few upper centimeters of the soil habitat, notably in the litter and humus layer (TAKEDA, 1978; HÅGVAR, 1983; WOLTERS, 1983; BERG et al., 1998). The migration of Collembola to deeper layers is a well known avoidance behaviour, which is attributed to different factors according to the climatic characteristics of the areas where the different studies were conducted (HOPKIN, 1997).

The classification of Collembola to ecomorphological life forms was introduced by GISIN (1943) and has been widely used ever since. Based on morphological characteristics, such as presence and number of eyes, pigmentation, length of the legs and the furca, species are characterised as euedaphic (species that are permanent soil dwellers), hemiedaphic (species that that live in the superficial soil layers and leaf litter) and atmobios (species that live in the surface and on vegetation). It was originally assumed that the morphological characteristics of a species reflect the soil layer preferred by it, but certain species have a life strategy that does not correspond to their life form (HÅGVAR, 1983, TAKEDA, 1995). On the other hand, a differentiation in the vertical preferences within a species has been reported (WOLTERS, 1983) indicating that smaller individuals tend to inhabit deeper layers.

In this study the following questions were addressed: are there vertical preferences for Collembola and under what circumstances does an avoidance behaviour occur? Are there species specific preferences and are they related to life forms? Does an intraspecific differentiation in vertical preferences occur that can be related to body size?

MATERIAL AND METHODS

Site description

The investigation site is located in north-eastern Greece, in the western part of the delta of the river Nestos (24° 43´ N, 40° 53´ E). The climate in the area is of the subcool-subhumid Mediterranean type, as defined by NAHAL (1981). Four types of deciduous forests can be distinguished in the area: a. Hardwood riparian forest, dom-

Corresponding author: V. Detsis, e-mail lsos2kok@auadec.aua.gr

inated *by Quercus pedunculiflora*, *Populus alba*, *Fraxinus angustifolia* and *Fraxinus oxycarpa*. b. Softwood-softwood riparian forest, dominated by *Populus alba*, *Salix alba*, *Alnus glutinosa* and *Ulmus minor*. c. Mixed stands without contact to the river, dominated by *Populus alba*, *Quercus pedunculiflora*, *Alnus glutinosa* and *Ulmus minor*. and d. Plantations of man-introduced hybrid poplars (*Populus canadensis*) plantations and d. mixed stands without contact to the river. All the stands grow on alluvial soil.

Sampling

The sites were sampled in July 1991, April 1992, January, April, August, September and November 1993, except for the softwood forest, which was sampled only in April and November 1993. In each sampling occasion 7 samples were taken from each forest type. The sampling design was stratified random. The samples consisted of the O-layer and a soil core 5 cm in diameter and 5 cm deep. Each sample was divided into three layers: the O layer, a layer 0-2.5 cm soil depth and 2.5-5 cm soil depth. The animals from each layer were extracted by means of a Berlese-Tullgren funnel.

Collembola animals were identified and counted and their body lengths measured. The biomass was calculated using the equations given by Tanaka (1970); Petersen (1975) and Teuben & Smidt (1992). When no equation was given for a certain species the one given for the taxonomically closest one was used (Wolters, 1983).

Soil temperature was measured immediately after each sample was taken at 5 cm depth with a digital point thermometer. Soil samples adjacent to those used for the extraction of the animals the ones mentioned above were taken to the laboratory and dried overnight at 103°C to determine water content. Biomass, soil temperature and soil water content were not determined in July 1991.

Statistics

Since the samples of the three layers resulted from the splitting of single soil cores, the differences in population densities in the different depths were tested with the Wilcoxon signed-rank test for tied samples (Sachs, 1972). Data from all samples were pooled for the purpose of this analysis.

The same procedure was undertaken with the data from the most abundant species to check whether the patterns observed reflect a tendency of the whole Collembola population or if there are species specific strategies. The results for four species that exhibit distinct seasonal strategies and belong to different families and life forms are presented here to illustrate the findings. Three of the species are classified as hemiedaphic (*Isotoma notabilis* Schäfer, 1896, *Cryptopygus thermophilus* Axelson, 1900 and *Ceratophysella engadinensis* Gisin, 1949) and one as euedaphic (*Protaphorura sp.*). The differences between mean individual biomass at different depths were tested for significance with the U-test.

Results

Soil water content and temperature data for the different sampling occasions are presented in Table 1. When the whole Collembola population is considered, most of the

TABLE 1

Mean soil water content and temperature ± Standard Deviation and Mean abundance per sample ± Standard Deviation of *Collembola* in the different layers. Significance levels (Wilcoxon-Test) *: p < 0.05, **: p < 0.01, ***: p < 0.001. Asterisks in the 2.5–5 cm and 0-2.5 cm columns concern differences between these layers and the 0-2.5 cm and O layers respectively. Asterisks in the O layer columns concern differences between this layer and the 2.5–5 cm one.

	Soil water content (%)	Soil temperature (°C)	Individuals			Biomass (μg)		
			2.5-5 cm soil	0-2.5 cm soil	O layer	2.5-5 cm soil	0-2.5 cm soil	O layer
July 91	-	-	20±31 **	27±37	42±85	-	-	-
April 92	32,3±12.5	15,5±3,6	19±32 ***	56±82	32±41 *	23,4±48,2 **	50,7±64,9	54,2±66,7 *
Jan. 93	33,3±16,6	2,4±1,6	14±23 **	27±29	32±44 **	27,9±43,8 *	55,1±66,1	77,5±84,6 ***
April 93	32,1±12,0	10,6±3,4	15±27 ***	56±76	46±57 ***	16,6±23,7 **	68,0±90,0	86,8±110,0 ***
Aug. 93	7,3±6,6	24,8±5,7	40±68	10±10 **	2±3 ***	41,2±70,0	21,1±22,7	6,3±10,7 ***
Sept. 93	21,1±20,0	19,0±1,2	17±22	29±27	49±53 *	16,0±17,8	43,1±50,5	91,3±137,8 **
Nov. 93	28,1±15,8	5,8±2,9	8±13 ***	27±26	29±27 ***	16,7±35,0 **	50,8±46,1	112,1±170,4 ***

TABLE 2

Mean abundance per sample ± Standard Deviation of four Collembola species in the different layers. Significance levels (Wilcoxon-Test) *: $p < 0.05$, **: $p < 0.01$. Asterisks in the 2.5–5 cm and 0-2.5 cm columns concern differences between these layers and the 0-2.5 cm and O layers respectively. Asterisks in the O layer columns concern differences between this layer and the 2.5–5 cm one.

	Isotoma notabilis			***Cryptopygus thermophilus***			***Ceratophysella engadinensis***			***Protaphorura sp.***		
	2.5-5 cm soil	**0-2.5 cm soil**	**O layer**	**2.5-5 cm soil**	**0-2.5l cm soil**	**O layer**	**2.5-5 cm soil**	**0-2.5l cm soil**	**O layer**	**2.5-5 cm soil**	**0-2.5 cm soil**	**O layer**
July 91	0±1 *	3±3	11±22 **	0±1	6±9	49±87	8±10	5±6	2±2	1±1	4±1	10±7
April 92	3±5 **	13±12	11±16 *	0	7±0	0	1±2	2±1	4±4	9±12	5±5	2±2
Jan. 93	4±8 **	9±13	8±12	3±1	18±8	8±7	1±2	3±3	6±8	4±6	8±8	9±12 *
April 93	5±10 **	16±22	12±11 **	7±9	21±13	44±48	8±14	34±56	17±51	2±5	8±9	12±24
Aug. 93	9±17 *	2±7	0±1 *	83±133	1±2	0	1±1	1±1	0	2±2	1±2	1±1
Sept. 93	6±8	16±24 *	32±32	28±28	8±7	36±44	2±2	1±3	2±3	1±2	12±20	29±51
Nov. 93	4±11 **	8±10	9±18 *	2±3	27±35	7±10	0±1 *	2±1 *	9±9 *	2±4	7±7	7±12

individuals as well as the greatest biomass were found in the upper soil layer and in the O layer (Table 1). The differences between the deeper soil layer and the upper ones were in most cases statistically significant. Differences were found between the upper soil and the O layer too and in most cases the population in the O layer was larger. These differences were statistically not significant and much smaller than the ones observed in the deeper soil layer. A single exception was August 1993. In this case most of the animals were found in the deeper layer. Generally the proportion of the individuals found in the deeper layer is greater than the proportion of the biomass found in the same layer, which indicates that the deeper layer is preferred by the smaller animals.

The pattern of vertical distribution observed at the species level coincides with the one observed for the whole Collembola population (Table 2). In August 1993 all species, regardless of their life-form classification retreated to the deeper layer. During all other sampling occasions, all species were generally more abundant in the surface layers, once again regardless of their life-forms. The large standard deviation observed is largely due to differences in the population between samples, and not to deviations from the observed vertical patterns.

Differences in mean biomass of the individuals inhabiting different layers were in most cases statistically significant and show that, for all species studied here, body size decreases with increasing depth, regardless of life forms (Table 3). There are two important features of this pattern. Firstly, results are consistent for all species and that invariably mean biomass decreases with increasing depth. Secondly, large standard deviation also exists that can be partly attributed to the pooling of data from different seasons and partly to an existing overlap in depth preferences.

TABLE 3

Mean biomass of individuals (μg of dry weight) ± Standard Deviation. Significance levels (U-Test) *: $p < 0.05$, **: $p<0.01$, ***: $p < 0.001$. Asterisks in the 2.5–5 cm and 0-2.5 cm columns concern differences between these layers and the 0-2.5 cm and O layers respectively. Asterisks in the O layer columns concern differences between this layer and the 2.5-5 cm one.

Species	**2.5-5 cm soil**	**0-2.5 cm soil**	**O layer**
Isotoma notabilis	1.17±0.96	1.29±1.34 ***	1.51±1.42 ***
Cryptopygus thermophilus	0.94±0.51 ***	1.52±1.32	1.59±1.16 ***
Ceratophysella engadinensis	1.05±1.10	1.15±1.11 ***	1.39±1.30 ***
Protaphorura sp.	3.56±4.06	3.58±3.15 *	4.03±3.96 *

DISCUSSION

The majority of Collembola was found in the upper soil layer and in the O layer in all cases except in August 1993. It has been suggested that the maximum population density is observed there, where the maximum decomposition activity takes place (WALLWORK, 1970). HASSALL et al. (1986) suggested that the hyphal mass is more easily accessible to Collembola in the litter and fermentation layers. A preference might also exist for early colonising microorganisms. If changes in their habitat occur, Collembola can react quickly and change their vertical distribution within a few hours (WHITFORD et al., 1981; HASSALL et al., 1986). Drought seems to be the factor that triggered the downward migration in August 1993 (TAKEDA, 1978; HASSALL et al., 1986; BERG et al., 1998 but see FABER & JOOSSE, 1993).

In a comparative study SGARDELIS et al. (1993) found that in Mediterranean ecosystems Collembola survived the summer drought period in an inactive state, which results in a population density close to zero. On the contrary in temperate ecosystems no significant population reduction was observed but rather a retreat of Collembola to deeper soil layers. The results of this study indicate that the Collembola population of the Nestos forests lies between these two extremes: a significant reduction in the population density is observed (although without coming close to zero) as well as a retreat to deeper layers.

In the two winter sampling occasions in January and November 1993 most animals were found in the surface layers. The air temperatures during sampling in November and January 1993 were much lower than the mean air temperature for these months and the long term average; in the latter case the soil was even partly covered by snow. USHER (1970) observed a downward migration in winter that was attributed to low temperatures. The lowest temperatures that occurred in the area during this study should present no substantial problem for Collembola.

All four species studied show the same pattern as the whole population. No vertical specialisation was observed. At the most, there was a slight tendency of *Ceratophysella engadinensis* and *Protaphorura sp.* to live somewhat deeper than the rest. In other studies too, only minor differences on the scale of millimetres were found in the "mean depth" for a number of species. They were so minor that a large overlap always existed (USHER, 1970; FABER & JOOSSE, 1993). HÅGVAR (1983) also observed a great overlap and a periodical appearance of almost all species in the higher layers.

Although according to its morphological characteristics *Protaphorura sp.* is classified as euedaphic, there were only minor differences in its vertical distribution compared to the other species. It was already observed in other studies (HÅGVAR, 1983) that some Collembola species, which are classified as euedaphic, do prefer the surface soil layers. TAKEDA (1978; 1995) observed that species with different life forms reach their maximum abundance level in the same depth. *Protaphorura sp.* is a large species, which is a common feature of species that prefer the upper part of the soil profile (TAKEDA, 1978; HÅGVAR, 1983). All the above do not suggest that species with euedaphic life forms generally prefer the surface soil layers, but that some of them do, and that life form is not necessarily restrictive in this context.

A general tendency of the smaller individuals of the same species to live deeper was observed (WOLTERS, 1983). Therefore, there are two possible explanations. The first is directly related to body size: the larger animals cannot find enough space in the deeper layers and stay in the surface layers where crevices are bigger (HÅGVAR 1983), whereas smaller animals, being more sensitive to desiccation have to stay deeper. The second explanation is that the eggs are laid in deeper layers and so the proportion of juveniles there is larger (DUNGER, 1983). It seems that, apart from the drought avoidance behavior, body size is the decisive factor controlling vertical distribution. This applies to the whole Collembola population and to the populations of the different species as well.

ACKNOWLEDGEMENTS

I wish to thank two anonymous referees for critical comments on an earlier draft and Mr. N. Orfanos for linguistic improvement of the text. The practical part of this work was carried out at the University of Essen, Laboratory of Zoology, while I received financial support from the German Academic Exchange Agency (DAAD).

REFERENCES

BERG, M.P., J.P. KNIESE, J.J.M. BEDAUX & H.A. VERHOEF (1998). Dynamics and stratification of functional groups of micro- and mesoarthropods in the organic layer of a Scots pine forest. *Biol. Fertil. Soils*, 26:268-284.

DUNGER W., (1983). *Tiere im boden*. A. Ziemsen Verlag, Wittenberg Lutherstadt, 280 pp..

FABER, J.H. & E.N.G. JOOSSE (1993). Vertical distribution of Collembola in a *Pinus nigra* organic soil. *Pedobiologia*, 37: 336-350.

GISIN, H. (1943). Ökologie und Lebensgemeinschaften der Collembolen im schweizeirischen Exkursionsgebiet Basels. *Rev. Suisse de Zool.*, 50:131-224.

HÅGVAR, S. (1983). Collembola in Norwegian coniferous forest soils. II. Vertical distribution. *Pedobiologia*, 25:383-401.

HASSALL, M., S. VISSER, D. PARKINSON (1986). Vertical migration of *Onychiurus subtenuis* (Collembola) in relation to rainfall and microbial activity. *Pedobiologia*, 29:175-182.

HOPKIN, S.P., (1997). *Biology of the Springtails (Insecta: Collembola)*. Oxford University Press, Oxford, New York, Tokyo, 330 pp..

NAHAL, I. (1981). The mediterranean climate from a biological viewpoint. In: DI CASTRI, D., D.W. GOODAL & R.L. SPECHT (eds), *Mediterranean-type shrublands*. Elsevier, Amsterdam, Oxford, New York, Tokyo: 63-86.

PETERSEN, H. (1975). Estimation of dry weight, fresh weight and calorific content of various collembolan species. *Pedobiologia*, 15:222-243.

SACHS, L. (1972). *Statistische Auswertungsmethoden*. Springer Verlag, Berlin, Heidelberg, New York, 545 pp..

SGARDELIS, S.P., S. SARKAR, M.D. ASIKIDIS, J.P. CANCELA DA FONSECA & G.P. STAMOU (1993). Phenological patterns of soil microarthropods from three climate regions. *Eur. J. Soil Biol.*, 29:49-57.

TAKEDA, H. (1978). Ecological studies of collembolan populations in a pine forest soil. II. Vertical distribution of collembola. *Pedobiologia*, 18:22-30.

TAKEDA, H. (1995). Changes in the collembolan community during the decomposition of needle litter in a coniferous forest. *Pedobiologia*, 39: 304-317.

TANAKA, M. (1970). Ecological studies on communities of soil Collembola in mt. Sobo, southwest Japan. *Jap. J. Ecol.*, 20: 102-111.

TEUBEN, A. & G.R.B. SMIDT (1992). Soil arthropod numbers and biomass in two pine forests on different soils, related to functional groups. *Pedobiologia*, 36:79-89.

USHER, M.B. (1970). Seasonal and vertical distribution of a population of soil arthropods: Collembola. *Pedobiologia*, 10: 224-236.

WALLWORK, J.A., (1970). *Ecology of soil animals.* McGraw-Hill, London, 283 pp..

WHITFORD, W.G., D.W. FRECKMAN, N.Z. ELKINS, L.W. PARKER, R. PARMALEE, J. PHILLIPS & S. TUCKER (1981). Diurnal migration and responses to simulated rainfall in desert soil microarthropods and nematodes. *Soil Biol. Biochem.*, 13: 417-425.

WOLTERS, V. (1983). Ökologische Untersuchungen an Collembolen eines Buchenwaldes auf Kalk. *Pedobiologia*, 25: 73-85.