European Journal of Soil Biology 82 (2017) 88–97

Contents lists available at ScienceDirect

European Journal of Soil Biology

journal homepage: http://www.elsevier.com/locate/ejsobi

# Arthropods in the subsoil: Abundance and vertical distribution as related to soil organic matter, microbial biomass and plant roots

Anton M. Potapov [a, *], Anton A. Goncharov [a], Eugenia E. Semenina [a], Anastasiya Yu Korotkevich [a, b], Sergey M. Tsurikov [a], Oksana L. Rozanova [a], Alexander E. Anichkin [a], Andrey G. Zuev [a], Ekaterina S. Samoylova [a], Irina I. Semenyuk [a], Ilya V. Yevdokimov [c], Alexei V. Tiunov [a]

[a] A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky Prospect 33, 119071 Moscow, Russia
[b] Moscow State Pedagogical University, Kibalchicha Str. 6, 129164 Moscow, Russia
[c] Institute of Physicochemical and Biological Problems in Soil Science, Russian Academy of Sciences, Institutskaya Str. 2, 142290 Pushchino-on-Oka, Russia

ARTICLE INFO

*Article history:*
Received 7 June 2017
Received in revised form
20 August 2017
Accepted 1 September 2017
Available online 14 September 2017

Handling editor: Stefan Schrader

*Keywords:*
Deep soil
Microarthropods
Mesofauna
Macrofauna
Soil animals
Carbon cycle

ABSTRACT

Large pools of organic carbon are stored in deep soil horizons (subsoil). Decomposition of soil organic matter (SOM) is driven by microorganisms that are in turn grazed by metazoan animals. Microbial populations and animal food webs in the soil are both at least partly dependent on labile organic carbon provided by plant roots. In this study, we described the vertical distribution of total $C_{org}$, microbial biomass, root biomass and the density of soil arthropods in deep layers (down to 110–210 cm depth) of three soils formed under the south taiga, broadleaved forest and forested steppe vegetation. By modeling the vertical distribution of animal population we estimated the soil depths above which 90% of the animals live (SD90 values). These values were the highest for Collembola, Protura and Symphyla (43–116, 69–144 and 54–95 cm, respectively, across the study locations), but relatively low for Acari (32–55 cm). In the forested steppe, less than 50% of all microarthropods and less than 10% of all insects inhabited litter and the uppermost 10 cm of mineral soil. Using generalized linear mixed-effect models we showed that the distribution of Collembola in the subsoil (below 30 cm) depended on root biomass and total $C_{org}$ content, while the distribution of mites was affected by total $C_{org}$ content and microbial biomass. The density of collembolans correlated significantly with root biomass both in the upper and lower parts of the soil profile. This suggests that soil fauna are involved in deep soil C cycling largely via grazing on root-associated microorganisms.



## 1. Introduction

Animal and microbial populations are mainly concentrated in topsoil layers. Consequently, studies on the diversity and ecology of soil animals rarely involve more than the upper 25 cm of the soil profile [1,2], even if a 'vertical distribution' is studied [3,4]. Animal communities in the deeper soil layers are generally overlooked, although the deep soil fauna is potentially involved into soil organic matter (SOM) dynamics either by direct consumption of SOM [5–7] or by altering the microbial community composition [8,9].

Here we use the term 'subsoil' to denote the soil layers below 30 cm. Several specialized taxa of Collembola, Oribatida, Diplura and Protura can be relatively abundant in the subsoil [2,10–12]. These small arthropods inhabit soil crevices, as well as voids and burrows created by decomposing plant roots, earthworms and other larger animals [13]. Indeed, the distribution of mites in the subsoil has been found to be affected by soil porosity [10]. Another factor that clearly influences the distribution of microarthropods in the soil is the total carbon content [14] that generally correlates with microbial biomass [15]. Soil microorganisms remain quite numerous and active well below 1 m depth, even though their total abundance is about 1.5–2 orders of magnitude lower than in the topsoil [16,17]. This creates a potential food source for soil microbivorous animals living in the deep soil. Microbial activity in the subsoil is strongly driven by the inputs of labile organic carbon provided by plant roots [18–20]. Similarly, even in the upper soil

* Corresponding author.
*E-mail address:* potapov.msu@gmail.com (A.M. Potapov).

http://dx.doi.org/10.1016/j.ejsobi.2017.09.001
1164-5563/

horizons a large proportion of soil arthropods can receive root-derived carbon directly or via feeding on root-associated microorganisms [21–25]. The role of the root-derived carbon can be even more important in the C-poor deeper soil horizons [26,27]. Therefore, the vertical distribution of deep soil animals is expected to be related to the distribution of plant roots. To our knowledge, no study has focused on the relationship between the main potential carbon pools (soil organic matter, fine root and microbial biomass) and the density of soil animals in the subsoil.

Microbial activity in mineral soil can vary within small distances creating 'hotspots' that appear e.g. due to a localized input of labile organic compounds by plant roots [28,29] or by a translocation of litter into mineral soil by burrowing animals [30,31]. Since the density of roots and zoogenic structures is low in the deep soil horizons, hotspots of microbial activity could be relatively infrequent. In this case, organic substrates can become spatially isolated from decomposer organisms ('decomposition mosaic') and are degraded slowly [32]. This results in a strongly heterogeneous distribution of SOM and microbial populations in deep soil horizons. Consequently, 'averaged' microbial parameters estimated using homogenized aliquots provide biased information on the real microbial activity. On the other hand, a quite large volume of soil is needed for extracting mesofauna and, especially, macrofauna from deep soil layers where they can not be abundant. We therefore expected that because of this technical constraint the estimated correlation between SOM content, microbial activity and the abundance of soil animals should be less pronounced in deeper soil layers than in the topsoil.

Here we present data on the distribution of soil-dwelling arthropods in the subsoil of three soil types formed under the south taiga, broadleaved forest and forested steppe and differing strongly in SOM content, profile depth and other features (Fig. 1S). We estimated the densities of soil animals throughout the main root layer (to 110–210 cm depths, depending on the soil type) along with the total organic carbon content, basal respiration, fine root biomass and microbial biomass. Our main objectives were (1) to describe the vertical distribution of arthropods in the mineral layers of three different soils, and (2) to reveal correlative relationships between the distribution of different groups of soil arthropods in the subsoil and the abundance of potential carbon sources (soil organic matter, root biomass and microbial biomass). We hypothesized that animals in the subsoil should depend largely on the root-derived carbon, and therefore the abundance of arthropods in the subsoil should be related to the abundance of plant roots. In addition, we tested the suggestion that the strength of the correlation between the density of soil animals and microbial activity in the bulk soil should decrease with depth.

## 2. Materials and methods

### 2.1. Study sites and sampling

The study was conducted in the European part of Russia. Three locations representing three different ecosystem types were sampled in August–October 2014: a south taiga forest, a broadleaved forest and a forested steppe forest. At each location, two or three trenches were excavated. In each trench, two or three soil columns were sampled; altogether, 21 columns were studied across all locations (Table 1). Soil samples were taken every 10 cm from the bottom to the top of the soil columns using a rectangular stainless steel corer (volume 640 $cm^3$). Two or three (according to the number of soil columns) samples of litter (50 × 50 cm) were collected near each trench.

### 2.2. Sample processing

Soil animals were extracted from, and root biomass measured in each soil core. Before the extraction of soil animals, four subsamples (ca. 5 ml each) were taken from each soil core, mixed and homogenized. These samples were used to estimate the total organic carbon content, microbial biomass and basal respiration (Table 2). The carbon content, basal respiration, microbial biomass and root biomass were measured in the mineral soil only. The abundance of soil animals was measured both in litter and mineral soil samples. Soil humidity was calculated in each sample using the difference between the soil before (wet soil) and after (dry soil) animal extraction. All parameters were recalculated on the dry weight basis.

The main groups of Arthropoda found in deep soil layers included Tullbergiidae and Isotomidae (Collembola), Acariformes and Parasitiformes (Acari), Cecidomyiidae, Mycetophilidae, Sciaridae and Ceratopogonidae (Diptera), Megaspilidae, Braconidae, Ceraphronidae, Chalcidoidea (Hymenoptera), Homoptera, Coleoptera, and Symphyla.

### 2.3. Statistical analysis

Animal densities were expressed as the number of individuals per 0.1 $m^3$, i.e. the number of individuals per $m^2$ in a 10 cm-thick layer of soil (= 1 × 1 × 0.1 m). To calculate the total density of soil arthropods, data from each soil column were integrated across the whole soil profile and expressed as the number of individuals per 1 $m^2$ of the soil surface. Due to the lack of normality, median values along with quartiles (25th and 75th percentiles) rather than mean values are reported.

To illustrate general trends in the vertical distribution of soil arthropods, total $C_{org}$, root biomass, and microbial biomass, the Local Polynomial Regression Fitting was applied to column data using *stat_smooth* in *ggplot2* package in R [36]. To draw null values using a logarithmic X-scale, 1 ind. 0.1 $m^{-3}$ (for the density of animals), 1 g C $kg^{-1}$ (for total $C_{org}$) or 1 mg C $kg^{-1}$ (for the root and microbial biomasses) were added to all values. The vertical distributions of total $C_{org}$, root biomass, microbial biomass, and of the density of soil animals were also compared using the 'proportion of maximum' units. To this end, values obtained in each soil layer were divided by the maximum observed for this parameter in this location.

Depth-related changes in the density of Collembola, Acari, Symphyla, Protura, and Insecta were described for each location separately using Generalized Linear Model with negative binomial distribution and zero inflation as implemented in AD Model Builder in *glmmADMB* package in R [37]. Depth-related changes in the total organic C, root biomass, microbial biomass and basal respiration were described for each location separately using Generalized Linear Model with Gamma distribution (natural logarithm link) using *glm* in R. The litter layer was excluded from these calculations. Predicted values for animals and soil parameters were derived for the first 300 cm of the soil profile. Using the cumulative proportion of predicted values soil depths at which 75% (SD75) and 90% (SD90) of animals lived [2] were estimated.

To assess which factors mainly affected the number of Collembola and Acari in the subsoil (below 30 cm) we constructed Generalized Linear Mixed-Effect Model as implemented in AD Model Builder in *glmmADMB* package in R [37]. Due to the overdispersion of non-zero count data we chose a negative binomial distribution; due to many zero records a zero-inflated model was used [38]. Numbers of soil animals in a sample were treated as the