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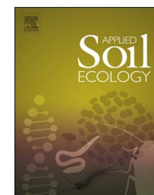

Distribution of prokaryotic communities throughout the Chernozem profiles under different land uses for over a century

Mikhail V. Semenov[a,*], Timofey I. Chernov[a], Azida K. Tkhakakhova[a], Alena D. Zhelezova[a], Ekaterina A. Ivanova[a,b], Tatyana V. Kolganova[a,c], Olga V. Kutovaya[a]

[a] Department of Soil Biology and Biochemistry, V.V. Dokuchaev Soil Science Institute, Moscow 119017, Russia
[b] Laboratory of Microbiological Monitoring and Bioremediation of Soils, All-Russia Research Institute for Agricultural Microbiology, Saint-Petersburg 196608, Russia
[c] Institute of Bioengineering, Research Centre of Biotechnology, Russian Academy of Sciences, Moscow 119071, Russia

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ABSTRACT

Land use affects physical, chemical and biological properties and processes in soil. Long-term field experiments were employed to reveal changes of soil characteristics induced by land use. Using high-throughput 16S rRNA gene amplicon sequencing and quantitative PCR, comparative analyses were conducted on prokaryotic community structure in different soil diagnostic horizons of Chernozems under forest, fallow and arable land within a long-term field experiment established by V.V. Dokuchaev in 1892. Soil organic carbon (SOC) was a more sensitive and reliable indicator of changes than microbial diversity indexes. *Verrucomicrobia* changed most among different prokaryotic phyla. Long-term tillage did not result in detectable changes in α-diversity of Chernozem prokaryotic communities, except for that plow pan horizon that showed a pronounced decrease in microbial diversity. The differences in prokaryotic community structure between soil horizons were more contrasting than between land uses. Analysis of β-diversity indicated that soil microbial communities at different depths formed non-overlapping clusters of A and B horizons, while microbiomes of transitional AB horizons fall in between these two clusters. The sharp decline in α-diversity in the plow pan horizon, as well as significant differences between the communities of A and B horizons indicate that the soil microbiomes are horizon-specific.

1. Introduction

Soil is the most complex environment with greatest microbial diversity (Nannipieri et al., 2003; Torsvik and Øvreås, 2002). Bacterial and archaeal communities play essential roles in many soil processes, e.g., participating in biogeochemical cycles and maintaining soil health (Basak and Biswas, 2010; Chaparro et al., 2012; Pereira e Silva et al. 2013; van Bruggen et al., 2017). Most of soil microbes (up to 80–99%) cannot be identified and characterized by culture-dependent techniques (Amann et al., 1995), however, novel molecular approaches, such as real-time PCR and high-throughput sequencing enable to identify and quantify many uncultivable and minor species of soil microbiota (Fierer et al. 2005; Jones et al. 2009), as well as to discover the linkages between soil and its microbial community (Morales and Holben, 2011).

Soil properties are the important ecological factors that control composition and activity of soil prokaryotic communities through various endogenic physiological and biochemical processes (Upchurch et al. 2008; Gattinger et al., 2002; Smalla et al., 2001). It is well known that soil microbial communities are influenced by a wide range of ecological factors, such as pH, soil organic matter quantity and quality, plant cover, moisture availability, temperature and aeration (Eilers et al., 2012; Fierer and Jackson, 2006; Lauber et al., 2009; Rousk et al., 2010; Loeppmann et al., 2016).

Although microorganisms inhabit the whole soil profile, our knowledge on structure and diversity of soil microbial communities is mostly limited to uppermost soil horizons, while microbial communities of deeper soil horizons are not still narrowly studied (Eilers et al., 2012). According to some estimations, subsurface horizons contain up to 35–50% of the soil microbial biomass (Fierer et al., 2003; Schutz et al., 2010; van Leeuwen et al., 2017). Because of significant changes in physical and chemical soil properties with depth, it is obvious to expect strong shifts in microbial community structure from surface to sub-surface soil horizons. Therefore, it is necessary to study the full soil profile for the complete estimation of the soil microbial diversity.

There are two main approaches to study the vertical distribution of soil microbial communities. The first approach is based on nominal separation of soil layers by uniform depths, while the second one distinguishes soil diagnostic (or genetic) horizons. The first approach

* Corresponding author at: Dept. of Soil Biology and Biochemistry, V.V. Dokuchaev Soil Science Institute, Pyzhyovskiy Lane 7, Building 2, Moscow 119017, Russia.
E-mail addresses: mikhail.v.semenov@gmail.com, semenov_mv@esoil.ru (M.V. Semenov).

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predominates in the most soil microbial ecology studies (Blume et al., 2002; Eilers et al., 2012; Fierer et al., 2003), due to its universalism and capability to estimate and compare microbial biomass in soil profiles with various vertical differentiation patterns. The second approach takes into consideration genetic formation of distinct horizons across soil profile (Rogers and Tate, 2001; Semenov et al., 2016; Will et al., 2010; Chernov et al., 2017; Kutovaya et al., 2015; van Leeuwen et al., 2017), which is used for soil diagnostics and classification (Classification and Diagnostics of Soils of the Soviet Union, 1977; IUSS Working Group WRB, 2015). The second approach is less convenient for the comparative studies of microbial communities in soils across spatial gradients. However, the differentiation of soil into distinct diagnostic horizons enables to link microbial community structure and soil-forming processes and soil properties which vary greatly in different soil horizons. Soil microbial community structure and its dominant taxa may be horizon-specific, which was shown by high-throughput sequencing of soil DNA (Will et al., 2010). In most cases, microbial diversity of upper organo-mineral horizons (A) is higher than in deeper mineral horizons (B) (Will et al., 2010). Moreover, variation between microbial communities structure in distinct horizons across single soil profile can be more prominent then variation across surface soils from a wide range of biomes (Eilers et al., 2012; Chernov et al., 2017). Thus, considering diagnostic horizons can be a prospective approach to study the vertical distribution of microbial communities throughout the soil profile.

Soils under different land-use types significantly vary in physical, chemical and biological properties, and, as a consequence, in microbial functioning and diversity (Lauber et al., 2009; Sala et al., 2000). An overwhelming number of studies have revealed effects of land use on soil microbial communities, e.g., shift in the abundances of different microbial groups depending on dominant plant species, agricultural practices, or the application of organic and mineral fertilizers (Jangid et al., 2008; Will et al., 2010; McCaig et al., 2001; Lauber et al., 2009). However, as it was mentioned above, soil microbial community responses to land-use effects were tested mostly for surface horizons.

Although the geography of soil microbial communities studies based on soil DNA high-throughput sequencing covers nearly all regions of the world, extremely diverse soils of Russia are still poorly investigated by this method (Chirak et al., 2013). At the same time, soils of European part of Russian Federation are well studied from the genetic soil science point of view, including the linkages between soil properties and soil forming factors. One of the most well-studied and famous Russian areas is “Kamennaya Steppe” nature reserve territory which represents a unique sequence of long-term field experiments established by V.V. Dokuchaev in 1892. In contrast to long-term field experiments on Rothamsted Station, whereas a wide range of molecular studies on soil microbiome were investigated (Hirsch et al., 2009; 2016; Zhalnina et al., 2015), soil microbial communities of “Kamennaya Steppe” have been extremely poorly studied.

In this study, we performed the comparative analysis of soil microbial communities structure throughout the full profiles of Chernozem soils located on the territory of “Kamennaya Steppe”. We wanted to determine the soil microbial communities shifts after more than a hundred years of being under forest, fallow and arable land. To study variation in microbial communities at different parts of soil profile, we have applied the soil diagnostic horizons approach. As microbiological parameters of soils, we estimated prokaryotes taxonomic composition, microbial diversity indexes, and the abundances of archaeal and bacterial genes by high-throughput 16S rRNA gene amplicon sequencing and quantitative real-time PCR.

2. Materials and methods

2.1. Soils and sampling sites

Soil samples were collected on the territory of agroecological station “Kamennaya Steppe” in July 2014. With a total area of 5232 ha, “Kamennaya Steppe” is located on south-west of Voronezh region on interfluvial plain between Bityug and Hoper rivers. The relief of the station is an undulating plain with mild-slope gullies and unshaped depressions. Climatic conditions are moderate continental, with cold winters and warm dry summers, and insufficient moistening. Average annual precipitation is about 420–440 mm. The average air temperature is -9.4 °C in January and −9.7 °C in February. The warmest month is June, with the average temperature of +20.1 °C. Vegetation period lasts 188 days. During winter months, soil freezes down to the depth of 60 cm.

Three full soil profiles under different land-use types were considered: 1) arable land (long-term field experiment from 1892) under winter wheat after harvesting (N 51°01′44″, E 40°43′29″); 2) fallow land (from 1882) under herbs and cereals with domination of *Festuca valesiaca*, *Bromus arvensis*, *Elytrigia repens*, *Poa arvensis*, and *Achillea millefolium* (N 51°01′51″, E 40°43′39″); 3) forest (planted in 1903) with *Quercus robur* and *Acer platanoides* as dominant species (N 51°1′41″, E 40°43′31″). Deep tillage of arable soil was annually performed. Field crop rotation included cereals (wheat, barley, maize) and tuber crops (sugar beet, sunflower). Mineral fertilizers were applied at a rate of 45–60 kg NPK ha^{-1}. Rainfall of 0.8 mm occurred nine days before soil sampling.

All three soils were classified as Typical Chernozems (Classification and Diagnostics of Soils of the Soviet Union, 1977), or Haplic Chernozems (Pachic, Clayic) (IUSS Working Group WRB 2014). The detailed description of soil profiles morphology is given in Appendix A in Supplementary materials.

Soil samples (about 100 g of each sample) were collected from the middle parts of three soil profile walls (i.e. three spatial replicates per soil diagnostic horizon) and stored then at −70 °C for further DNA extraction and chemical analyzes. The distance between the sampling points within one diagnostic horizon was about 100 cm. The total soil organic C (TOC) and total N (TN) contents were estimated by Vario MACRO Cube CN-analyzer (Elementar Analysensysteme GmbH, Germany). Soil samples for organic carbon measurements were pretreated with 0.5 M HCl to remove carbonates (Harris et al., 2001). Soil pH was measured with a potentiometer in a 1:2.5 soil/water suspension. All chemical analyzes were performed to each of three spatial replicates. Particle size distribution analysis was performed with a Laser-Particle-Sizer «Analysette 22 comfort» (FRITSCH, Germany), equipped with a low-power (2 mW) Helium-Neon laser with a wavelength of 632.8 nm as the light source.

2.2. Soil DNA extraction and purification procedure

DNA was extracted and purified from 0.25 g of each spatial replicate using PowerSoil DNA Isolation Kit (Mobio Laboratories, Solana Beach, CA, USA) according to the manufacturer’s specifications. Homogenization of the soil samples was performed using Precellys 24 (Bertin Technologies, France). Extracted DNA samples were stored in −20 °C until further analyzes.

2.3. 16S rRNA archaeal and bacterial quantification

The relative abundances of bacterial and archaeal 16S rRNA gene copies were analyzed by quantitative PCR using EvaGreen Supermix (concentrated buffer with deoxyribonucleotides, Sso7d-fusion polymerase, $MgCl_2$, EvaGreen dye and stabilizers) (Bio-Rad, Hercules, USA) and 1 µl of template DNA. Cloned fragments of *Escherichia coli* and FG-07 *Halobacterium salinarum* ribosomal operons were used to prepare standard solutions of known concentrations. Primers Eub338 / Eub518 (Lane, 1991) and arc915f/arc1059r (Yu et al., 2005) were applied for bacteria and archaea, respectively.

The reaction was carried out in iCycler (Bio-Rad, Hercules, USA) using the following protocol: 94 °C for 15 min, followed by 40 cycles of

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