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SOIL BIOLOGY

Metagenomic Characterization of Biodiversity in the Extremely Arid Desert Soils of Kazakhstan

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Abstract—For the first time, the composition of microbiomes in the biological crust (AKL) horizons of extremely arid desert soils (Aridic Calcisols) developed from saline and nonsaline alluvial deposits in the Ili Depression (eastern Kazakhstan) was analyzed. To describe the diversity of microorganisms in the soil samples, a novel method of pyrosequencing (Roche/454 Life Sciences) was applied. It was shown that bacteria from the Proteobacteria, Actinobacteria, Firmicutes, Verrucomicrobia, Acidobacteria, and Bacteroidetes phyla predominate in all the samples; these are typical representatives of the microbiome of soil crusts. A distinctive feature of the extremely arid soils is the high contribution of cyanobacteria (25–30%) to the total DNA. In the soils developed from saline sediments, representatives from the Rubrobacteraceae, Streptococcaceae, and Caulobacteraceae families and from the Firmicutes phylum predominated. In the soils developed from nonsaline gypsiferous deposits, bacteria from the class of Acidobacteria, subgroup Gp3, of the Methylobacteriaceae family and the class of Subdivision 3 from the Verrucomicrobia phylum predominated.

Keywords: microbiome, soil DNA, sequencing, microbial communities, biodiversity, biological activity, biological crusts

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INTRODUCTION

The biological activity of extremely arid desert soils (Aridic Calcisols) that were described for the first time and separated at the soil type level by Efstifeev [7] is considered one of the key factors of pedogenesis and differentiation of the microprofile of these soils [3, 6, 29]. The surface of extremely arid soils is covered by the so-called desert pavement, under which a vesicular crust horizon and a layered subcrust horizon are formed. According to the new Russian soil classification system [9], their paragenetic association is designated as the AKL (crust) horizon. Surface horizons of desert soils with a similar morphology are often considered biological crusts, because they represent complex biocenoses of algae [10, 35], bacteria [34], micromycetes [18], and, in some cases, mosses and lichens [22]. These surface horizons of extremely arid soils compose a significant part of living matter in the desert landscape and play the key role in the functioning of desert ecosystems [36]. They protect the soil from overdrying [22, 36] and wind erosion [10, 24]. The biological activity of microorganisms in the biological crusts ensures the fixation of nitrogen and carbon dioxide from the atmosphere in the areas with the low projective cover by higher plants, as in the studied extremely arid deserts of Kazakhstan.

The aim of our study was to characterize the prokaryotic microbial community of the extremely arid desert soils on the basis of the analysis of their metagenome.

The study of genetic materials obtained directly from the environmental objects is considered the main approach in the soil metagenomics. This is a powerful tool in ecology [19], which is applied to study and compare metabolic characteristics of complex microbial communities [16, 21]. The analysis of total DNA isolated from the soil samples makes it possible to judge the real composition and structure of the microbial community and to judge the biological diversity in the studied soil objects.

OBJECTS AND METHODS

This work continues the study of extremely arid desert soils and their microbiological and micromorphological properties initiated by us earlier [10].

Metagenome was examined in the soils on low piedmont plains along the periphery of the Ili Depression in eastern Kazakhstan. These plains are composed of the gravelly sandy and loamy fanalluvial sediments of varying thickness. From the surface, a continuous or discontinuous mantle of gravelly desert pavement is usually developed. The gravelly material

Table 1. Chemical properties of the topmost horizons of extremely arid soils

Horizon	Depth, cm	pH_{H_2O} (1 : 2.5)	Humus	CO_{2carb}	Gypsum	HCO_3^-	Cl^-	SO_4^{2-}	SO_{4toxic}^{2-}	Ca^{2+}	Mg^{2+}	Na^+	K^+	Sum of salts	Sum of toxic salts
			%			cmol(+)/kg								%	
Extremely arid soil developed from saline alluvial deposits (Solonchak)															
K (without gypsum)	0–3	9.1	0.18	3.56	0.12	0.42	2.79	0.44	0.00	1.35	0.35	3.22	0.02	0.251	0.23
Kcs (with gypsum)	0–3	8.7	0.18	5.1	0.87	0.48	8.88	10.20	0.00	11.30	0.19	5.76	0.17	1.238	0.62
L	3–10	8.7	0.39	4.14	0.17	0.24	7.14	5.30	0.00	5.80	0.13	5.76	0.11	0.790	0.49
Pit 4-06. Extremely arid soil developed from nonsaline gypsiferous alluvial deposits (Gypsisol)															
K	0–2	8.9	0	3.78	0.14	0.45	0.07	0.84	0.54	0.75	0.13	0.19	0.20	0.101	0.04
L	2–5	8.8	0	1.89	0.23	0.35	0.07	1.82	0.87	1.30	0.13	0.22	0.32	0.159	0.05

on the surface is covered by desert varnish. Under the gravelly pavement, a thin soil profile with a clear differentiation into the pale yellow or whitish vesicular crust, the layered subcrust, and the dense reddish brown middle-profile horizon is developed. The soils effervesce from the surface and contain gypsum in the upper 30 cm.

Piedmont plains at the foot of the Ul'ken-Bogutty Range encircling the Ili Depression belong to arid territories with the mean annual precipitation of less than 150 mm and with a high degree of climatic continentality: the annual range of temperatures reaches 82°C. The average air temperature of the cold season (from the end of September to March) is –3.5°C, and the average air temperature of the warm season is +21.2°C. The spring maximum of precipitation is clearly pronounced. The soils are subjected to freezing to the depth of 60–100 cm and remain in the frozen state for several months [12]. The soil water regime is dictated by the low precipitation against the background of the high potential evaporation reaching 1000–1300 mm/yr in the subboreal deserts [14]. Sharp contrasts in the degree of soil moistening are typical of this area. Though the soils remain in the dry state for most of the year, the active development of soil microorganisms and diverse biochemical processes take place during the short periods of high soil moistening lasting for several days [4, 5].

Higher plants are virtually absent in the areas of extremely arid desert soils; separate species of ilynia (*Ilynia regelii*) shrubs can be found along dry valleys of temporary water streams. The aridity of the soil climate might be enhanced by the gravelly desert pavement, whose surface in the summer warms up more than the surface of barren sands or loams [8]. Judging from the available descriptions of the soils in analogous landscapes of eastern Kazakhstan and Mongolia, extremely arid desert soils are confined to the areas with desert pavement on the soil surface.

Soil samples from the vesicular crust layer of the AKL horizon with the maximum manifestation of the biological activity (biological crust) of two soil pits—3-06 and 4-06—spaced 4 km apart from one another were taken for the metagenomic analysis. The AKL horizon is considered a diagnostic horizon of the extremely arid desert soils [9]. Data on the chemical properties of the AKL horizon with K (vesicular crust) and L (layered subcrust) subhorizons are presented in Table 1.

Isolation of DNA from the soil samples. Weighed soil samples (0.5 g) were mechanically ground with the use of glass balls in the following extracting buffer solution: 350 μL of solution A (sodium phosphate buffer, 200 mM; guanidine isothiocyanate, 240 mM; pH 7.0), 350 μL of solution B (Tris-HCl, 500 mM; SDS, 1 wt %; pH 7.0), and 400 μL of a mixture of phenol with chloroform (1 : 1). The destruction of the samples was performed for 40 s on a Precellys 24 homogenizer (Bertin Technologies, France) at the maximum power (6500 rpm (680 rad/s)) using 3D rotation. The obtained preparations were centrifuged at 16000 rpm (1700 rad/s) for 5 min. The water phase was separated and subjected to repeated extraction with chloroform. Then, the DNA precipitation was performed by adding equal volumes of isopropyl alcohol. After centrifuging, the precipitate was washed with 70% ethanol and dissolved in water at 65°C for 5–10 min. The purification of DNA was performed by the method of electrophoresis in 1% agaric gel with further isolation of DNA from the gel by the sorption on silicon oxide [1, 31].

Purified DNA preparations (10–15 ng) were used as a template in the PCR reaction with the following ther-

mal cycle: 95°C, 30 s; 50°C, 30 s; 72°C, 30 s (overall, 30 cycles). Encyclo polymerase (Evrogen Company, Russia) and universal primers 515F (GTGCCAGCMGCCGCGGTAA) and 806R (GGACTACVSGGGTATCTAAT) were added to the hypervariable region V4 of 16S-rRNA [17]. Oligonucleotide identifiers for each of the samples (overall, 20 identifiers) and sequencing kits developed for pyrosequencing according to the protocol of Roche Applied Science (Switzerland) were also added. The preparation of the samples and sequencing were performed on a GS Junior device (Roche, Switzerland) according to recommendations from the manufacturer.

The taxonomic identification of nucleotide sequences and the comparative analysis of microbial communities were performed with the use of the tools for the visualization and analysis of microbial population structure (VAMPS) available on the internet (http://vamps.mbl.edu). In the classification of nucleotide sequences, the database of the ribosomal database project (RDP) was applied (http://rdp.cme.msu.edu).

The analysis included the following procedures: discrimination of amplicon libraries according to the identifiers, quality control of sequencing and filtration of nucleotide sequences, combination of sequences into operational taxonomic units (OTUs) with the use of 97% similarity level, and sequence alignment using the UCLUST algorithm.

RESULTS

The applied primers were constructed on the basis of 16S-rRNA gene sequences of bacteria and archaea, which made it possible to perform a comprehensive analysis of the prokaryotic community.

Overall, 5684 sequences were obtained. The number of sequences from the soil samples reached 2644 (in the sample from pit 3-06) and 3040 (in the sample from pit 4-06). Thus, the average number of sequences from the soil samples was 2842. The total number of OTUs corresponding to the species taxonomic category comprised 152. They were grouped into 18 phyla and 101 families. Along with bacteria and archaea with identified taxonomic position, the soil samples contained unclassified sequences (UCSs), the portion of which was about 5.2–5.3%.

Analysis of nucleotide sequences at the domain level. At the level of domains, bacteria predominated in the samples (65.9 and 74.9%), though their portion was significantly lower in comparison with that in the less arid soils, where it reaches 94–100% [15]. Archaea were present as minor components (0.5% in the sample from pit 3-06 and 0.3% in the sample from pit 4-06).

Analysis of nucleotide sequences at the phylum level. The qualitative composition of bacterial and archaeal phyla was similar for both soils (Fig. 1a; hereinafter, data on the soil samples from pits 3-06 and 4-06 are compared). Dominant groups of bacteria in these two soils were represented by Proteobacteria (43.9 and 50.8%), Actinobacteria (9.5 and 10%), Firmicutes (2.4 and 0.8%), Verrucomicrobia (1.1 and 3%), Acidobacteria (1.1 and 2%), and Bacteroidetes (1.4 and 1.2%) phyla. The portions of other bacterial phyla were less than 1% (Table 2). The dominance of Proteobacteria, Actinobacteria, and Acidobacteria in the biological soil crusts was also noted by other researchers [33, 34]. It is probable that these bacterial phyla are representatives of the core component of the microbiome characteristic of most soil types of the world.

Archaea were represented by the Crenarchaeota phylum.

A distinctive feature of the extremely arid soils is the presence of the great number of cyanobacteria in the DNA of the microbial community. Their portions reached 33.6 and 24.7%. Thus, cyanobacteria become dominant organisms in the community of soil microorganisms. The same phenomenon was observed for some other arid soils [25].

In the studied soils, cyanobacteria play the major role in the immobilization of carbon during their photosynthetic activity [23]. Their active development may be one of the reasons for the formation of specific dark films on the soil surface (desert varnish) because cyanobacteria synthesize UV-absorbing pigment scytonemin [20].

Analysis of nucleotide sequences at the family level. The biogenome of the studied soils includes representatives of 27 families (Fig. 1b) with distinct dominants (Table 3): Cyanobacteria (33.6 and 24.7%); Enterobacteriaceae from the class Gammaproteobacteria (15.6 and 13.0%); Pseudomonadaceae (11.7 and 1.6%); the order of Myxococcales (0.9 and 13.2%), which is only found in desert soils; Moraxellaceae (0.7 and 8.1%); and Acetobacteraceae (3.2 and 2.9%) that are also endemic organisms.

Representatives of the Enterobacteriaceae and Pseudomonadaceae families were identified as dominants in the upper horizons of a light chestnut soil [15], whose properties are relatively close to the properties of brown desert soils. Representatives of the Acetobacteraceae family are known to prefer slightly acid media (pH 5.4–6.3) for their growth and development. However, in the extremely arid soils, they have adapted to a slightly alkaline medium (pH 8.7–8.9) (Table 1) owing to their capacity for fermentation of sugars actively produced by cyanobacteria [10, 26].

A comparative analysis of nucleotide sequences at the family level has also demonstrated certain differences in the structure of soil microbial communities between the studied soils.

Thus, in the sample from pit 3-06, the families of Rubrobacteraceae (from the class of Actinobacteria), Streptococcaceae (from the phylum of Firmicutes), and Caulobacteraceae (from the class of Alphaproteobacteria) were represented by 30 sequences (1% of the total number) each. The dominance of the Firmicutes phylum can be related to the presence of toxic salts. This

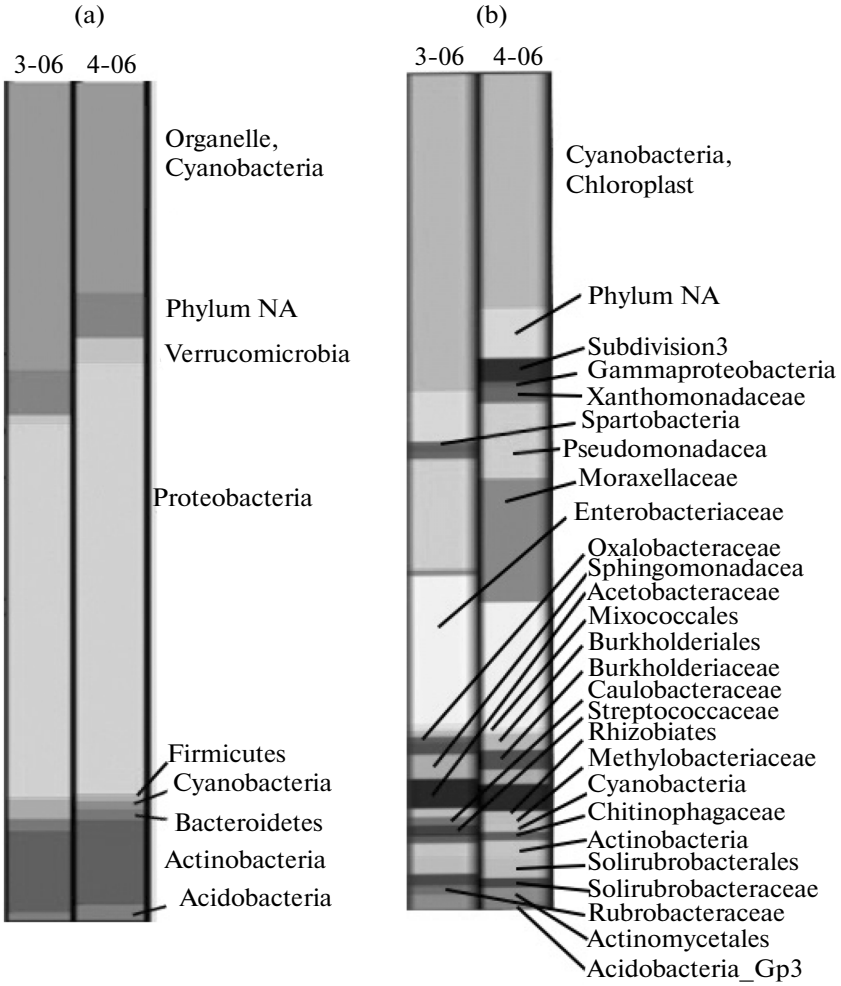

Fig. 1. The contribution of different (a) phyla and (b) families to the total taxonomic structure of microorganisms in the extremely arid soil.

soil is moderately salinized with sodium chlorides; the sum of toxic salts reaches 0.49% in the K horizon and 0.62% in the K_{CS} horizon. In contrast, the content of soluble salts in the soil described in pit 4-06 is no higher than 0.04%, except for the lowermost horizons, where the total salt content somewhat exceeds 1% owing to the presence of nontoxic gypsum [11].

These results are in agreement with the results obtained by other researchers, who also noted the dominance of representatives of the Firmicutes phylum in salt-affected soils [13, 27]. Many representatives of Actinobacteria are radiation-resistant organisms capable of metabolism in a medium subjected to strong ionizing radiation. Representatives of the Caulobacteraceae family are oligotrophic organisms: they can utilize nutrients in very low concentrations. These microorganisms may be fixed on the substrate surface forming specific biofilms for a more complete utilization of nutrient sources.

The soil described in pit 4-06 is characterized by the presence of bacteria from the class of Acidobacteria, subgroup Gp3, though their amount is relatively small in comparison with that in other soils [32]. These bacteria are *K*-strategists adapted to oligotrophic niches. Their presence in this soil is explained by the lower content of soluble salts and by some decrease in pH (in comparison with the soil of pit 3-06). Acidobacteria belong to halotolerant species; however, they were absent in the saline sample from pit 3-06.

Halotolerant bacteria of the Methylobacteriaceae family were also present in pit 4-06. Under these specific conditions, they can synthesize bacteriochlorophyll, so it is probable that these bacteria and phototrophic organisms are of the same origin [28]. Earlier, representatives of this family were described in soils of the coastal zone, which attests to a wide range of their ecological adaptations [13].

In the soil of pit 4-06, we determined 65 sequences (2.5%) of the class Subdivision 3 from the phylum Verrucomicrobia. In the soil of pit 3-06, there were 18 sequences (0.6%) from this phylum. Verrucomicrobia are free-living bacteria with aerobic heterotrophic

Table 2. Taxonomic composition of the microbial community in the topmost horizons of extremely arid soils at the phylum level

Domain	Phylum	Number of sequences	ortion, %	Number of sequences	ortion, %
		Pit 3-06		Pit 4-06	
Archaea	Crenarchaeota	9	0.30	1	0.04
	phylum_NA	5	0.16	8	0.30
Bacteria	Acidobacteria	32	1.05	53	2.00
	Actinobacteria	289	9.51	263	9.95
	Bacteroidetes	44	1.45	33	1.25
	Chlamydiae	4	0.13	Not found	
	Chloroflexi	1	0.03	2	0.08
	Cyanobacteria	12	0.39	24	0.91
	Deinococcus-Thermus	8	0.26	4	0.15
	Firmicutes	72	2.37	21	0.79
	Gemmatimonadetes	8	0.26	12	0.45
	Nitrospira	4	0.13	4	0.15
	OP10	Not found		1	0.04
	Planctomycetes	6	0.20	1	0.04
	Proteobacteria	1333	43.85	1343	50.79
	Verrucomicrobia	32	1.05	78	2.95
	phylum_NA	159	5.23	141	5.33
Organelle	Cyanobacteria	1022	33.62	653	24.70
Unknown	phylum_NA	Not found		2	0.08

metabolism that can utilize sulfates of polysaccharides [26]. This attests to their close relations with cyanobacteria—the main source of polysaccharides in soil.

In the soils of both pits (3-06 and 4-06), we found 36 and 54 sequences (1.2 and 2.1%, respectively) of unidentifiable bacteria from the Burkholderiales order. We suppose that they might belong to DNA of iron bacteria from the genus *Leptothrix*, belonging to the Burkholderiales order. These bacteria were earlier identified by us on fouling glass slides [10, 30].

CONCLUSIONS

For the first time, data on the metagenome of extremely arid soils in the Ili Depression of Kazakhstan have been obtained. These data reflect the real species diversity of the soil prokaryotic communities. It is probable that the reasons for the high biodiversity of these communities in the uppermost soil horizons are related to the competition of microorganisms for scarce trophic resources in desert substrates and to the high potential of microorganisms for adaptation to the conditions of ecological pessimum of their habitats. Under these conditions, the dependence of microorganisms on the major ecological factors—moisture deficiency, high temperatures, the absence of higher vegetation, and the presence of soluble salts in the substrat—is clearly manifested.

The microbiomes of the topsoil horizons in the two studied soil profiles have their own individual features. The differences in the taxonomic composition of microorganisms in these soils may be related to several reasons. First, this is the natural heterogeneity in the soil chemical properties; in particular, the salt content in the soil of pit 3-06 was considerably higher than that in the soil of pit 4-06. Second, this is the heterogeneity of the soils as microbial habitats resulting in the localization of vegetating forms of the microorgan-

Table 3. Taxonomic composition of the microbial community in the topmost horizons of extremely arid soils at the family level

Domain	Phylum	Class	Order	Family	Number of sequences	Portion, %	Number of sequences	Portion, %
					Pit 3-06		Pit 4-06	
Bacteria	Acidobacteria	Acidobacteria_Gp3	Unassigned	Unassigned	Not found		20	0.76
	Actinobacteria	Actinobacteria	Actinomycetales	family_NA	46	1.51	39	1.48
			Rubrobacterales	Rubrobacteraceae	30	0.99	Not found	
			Solirubrobacterales	Solirubrobacteraceae	40	1.32	29	1.10
				family_NA	51	1.68	52	1.97
			order_NA		48	1.58	52	1.97
	Bacteroidetes	Sphingobacteria	Sphingobacteriales	Chitinophagaceae	24	0.79	23	0.87
	Firmicutes	Bacilli	Lactobacillales	Streptococcaceae	30	0.99	Not found	
	Cyanobacteria	Cyanobacteria	order_NA	family_NA	Not found		24	0.91
	Proteobacteria	Alphaproteobacteria	Rhizobiales	Methylobacteriaceae	"		15	0.57
				family_NA	30	0.99	Not found	
			Caulobacterales	Caulobacteraceae	28	0.92	20	0.76
			Rhodospirillales	Acetobacteraceae	96	3.16	76	2.87
			Sphingomonadales	Sphingomonadaceae	78	2.57	39	1.48
		Betaproteobacteria	Burkholderiales	Burkholderiaceae	36	1.18	56	2.12
				Oxalobacteraceae	20	0.66	44	1.66
				Unassigned	19	0.62	16	0.61
		Deltaproteobacteria	Myxococcales	family_NA	6	0.86	350	13.24
		Gammaproteobacteria	Enterobacteriales	Enterobacteriaceae	474	15.59	344	13.01
			Pseudomonadales	Moraxellaceae	20	0.66	215	8.13
				Pseudomonadaceae	357	11.74	42	1.59
			Xanthomonadales	Xanthomonadaceae	24	0.79	16	0.61
			order_NA	family_NA	17	0.56	Not found	
	Verrucomicrobia	Subdivision3			Not found		65	2.46
		Spartobacteria			18	0.59	Not found	
	phylum_NA	class_NA			159	5.23	141	5.33
Organelle	Cyanobacteria	Cyanobacteria	Unassigned	Chloroplast	1022	33.62	653	24.70

isms in the loci with available nutrients and more favorable living conditions.

The obtained data attest to the significant role of the physicochemical factors and morphological specificity of the topsoils in the development of microbial communities in desert ecosystems, which takes place under conditions of the virtual absence of higher vegetation and humus components in the soil horizons.

The diversity of soil microorganisms specifies the wide range of ecological functions of the extremely arid soils, in which bio-abiotic interactions (according to [2]) between live (biotic) and inert (mineral) parts of the soil take place with the development of a clearly differentiated soil microprofile in the seemingly "lifeless" desert soils.

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