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EXPERIMENTAL ARTICLES

Successional Changes in the Microbial Community of the Alkaline Lake Khilganta during the Dry Season

Z. B. Namsaraev[a, *], V. M. Gorlenko[b], and S. P. Buryukhaev[c]

[a] *NRC Kurchatov Institute, Moscow, Russia*
[b] *Winogradsky Institute of Microbiology, Research Center of Biotechnology, Russian Academy of Sciences, Moscow, Russia*
[c] *Institute of General and Experimental Biology, Siberian Branch, Russian Academy of Sciences, Ulan-Ude, Russia*
**e-mail: zorigto@gmail.com*

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Abstract—Microbial processes in a shallow, saline, alkaline Lake Khilganta (Southern Siberia) were studied during the dry season. During the drought, a crust was formed on the lake surface, where low rates of production processes were observed, with predominance of anoxygenic photosynthesis at 2.3 mg C/(dm^3 day). The rates of microbial processes increased after short-term rains. During this period, a thin cyanobacterial mat was formed on the bottom, in which filamentous cyanbacteria *Geitlerinema* spp. predominated and the rate of oxygenic photosynthesis was up to 18 mg C/(dm^3 day). Subsequent water evaporation and salinity increase resulted in altered community types and their activity. Red spots emerged on the mat surface, where anoxygenic prototrophic members of the genus *Ectothiorhodospira* predominated. Anoxygenic photosynthesis became the main production process in microbial mats, with the rate of 60 mg C/(dm^3 day). At salinity increase to 200 g/L, the water remained in small depressions on the bottom, where extremophilic green algae *Dunaliella* sp. predominated, and the rate of oxygenic photosynthesis was 0.877 mg C/(dm^3 day). These changes in the type and activity of microbial communities is an example of succession of microbial communities in Southern Siberia saline lakes during drought.

Keywords: saline lakes, dry period, community succession, rates of microbial processes, photosynthesis, sulfate reduction, methanogenesis

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Succession is one of the basic ecological concepts, implying a process of change in the species structure at a certain site resulting from the action of environmental factors. In the course of succession, apart from sequential change of species and species associations, the abiotic components also change, affecting organic matter accumulation, mineral transformation, and modification of environmental parameters (Zavarzin, 2007). Research on succession processes in microbial communities is presently concentrated on the species composition of these communities and relationships between community composition and environmental factors, while investigation of the functional activity in the course of succession is relatively uncommon (Dupraz and Visscher, 2005; Navarro et al., 2009; Podell et al., 2014).

The microbial community in a saline, alkaline Lake Khilganta (Southern Siberia) was investigated. Extensive research of this lake was carried out during the moist period, when its parameters were relatively stable (Zavarzin, 1993; Gorlenko et al., 1993; Gerasimenko et al., 2003; Kompantseva et al., 2005; Namsaraev, B.B. and Namsaraev, Z.B., 2007; Tsyrenova et al., 2011a, 2011b). Since 2000, droughts occurred in the area of the lake location, resulting in its frequent drying up and the basin being filled only during short-termed rains. After the rain period, the basin became dry, with salinity increasing from 40 to at least 260 g/L in the course of several days (Namsaraev et al., 2010). Drastic changes of the water parameters in the lake enabled us to carry out research impossible at the stable state of the lake ecosystem and to investigate successional changes in the community. The goal of the present work was to investigate the functional activity of the Lake Khilganta microbial community in the course of succession processes caused by the alterations in lake water salinity.

MATERIALS AND METHODS

Subject of research. Lake Khilganta (50°42.535′ N, 115°06.086′ E) is located in the steppe zone in the southeastern Transbaikal area, at the divide of Onon and Aga rivers, 668 m above the sea level, and 76 km south to the Aginskoe settlement. The lake is drainless, round, with inclined shores. The maximal water area during the moist period is up to 0.3 km^2, the greatest water depth is 64 cm. The basin dries completely during the dry period.

Research techniques. The temperature, pH, and redox potential (Eh) were determined at the sampling site, as well as carbonate concentration (by titration) and salinity (refractometrically). The concentrations of chlorophyll *a* and bacteriochlorophyll *a* were determined by spectrophotometry (Namsaraev, 2009). The mineralogy of the bottom sediments was investigated using light microscopy (Namsaraev et al., 2010). The data on the weather and precipitation were obtained from the World Meteorological Organization database, Aginskoe weather station, WMOID 30859 (https://www. ncdc. noaa.gov/data-access/land-based-station-data/land-based-datasets). A moisture of the sediments was determined by drying at 105°C and weighing before and after drying (GOST 28268-89, 2009). The rates of photosynthesis and dark CO_2 fixation were determined in the samples supplemented with ^{14}C-bicarbonate. The rates of sulfate reduction were measured using ^{35}S-labeled sulfate (Kuznetsov and Dubinina, 1989; Gorlenko et al., 1999), and the rate of lithotrophic methanogenesis was measured using ^{14}C-labeled bicarbonate (Namsaraev et al., 1999). Carbon consumption for sulfate reduction and methanogenesis was calculated according to the known equations (Belyaev et al., 1981). The samples of water, microbial mats, crust, and bottom sediments in 20-mL glass vials were exposed for 12 h under in situ conditions of temperature and illumination. To determine the rate of photosynthesis, the samples were incubated under light, while for determination of the rates of dark CO_2 fixation, sulfate reduction, and methanogenesis they were incubated in the dark. To determine the rate of anoxygenic photosynthesis, the sample was supplemented with diuron. For calculation of production according to the known formula (Kuznetsov and Dubinina, 1989), only the carbon of dissolved bicarbonate was considered. This assumption was based on bicarbonate concentration exceeding that of carbonate and on expected slow redistribution of labeled bicarbonate between the natural and introduced bicarbonate. For determination of the rates of microbial processes in cyanobacterial mats and in the samples of green microalga *Dunaliella* sp., lake water collected at the time of sampling was added. The effect of salinity on the rates of production processes was studied in freshly collected mat samples, which were supplemented with lake water diluted with freshwater to desired concentration. The vials with crust samples were filled with freshwater in order to imitate rain precipitation, stored for 60 min until salt dissolution (final pH 8.18, salinity 50 g/L), supplemented with the radioisotope label, and incubated upon the lake bottom. For determination of the species composition of phototrophs, the samples were fixed with 4% formalin. For microscopy of the dry crust, the sample was homogenized on the slide, supplemented with 5% HCl for carbonate removal, and examined under a light microscope at ×400–1000 magnification. The following manuals were used for identification of cyanobacteria, green algae, and anoxygenic phototrophic bacteria, respectively: Komárek and Anagnostidis (2007), Dedusenko-Shchegoleva et al. (1959), and *Bergey's Manual of Systematic Bacteriology* (2005).

RESULTS

Climatic conditions and hydrochemistry of Lake Khilganta. The chemical composition, pH, and salinity of Lake Khilganta water depend on climatic conditions of the southeastern Transbaikal area. During moist years (before 1999), at the annual rainfall of up to 550 mm, the lake was filled with water of ~40–50 g/L salinity and pH 9.5–9.9, which belonged to the chloride-sulfate-sodium type. During dry years, including the sampling periods (259 and 152 mm in 2006 and 2007, respectively), the lake was usually completely dry. Water of saturated green color remained in small depressions at the lake bottom. In these depressions, salinity was 200–260 g/L, pH 7.2–8.1, and the water was of the chloride-sulfate-sodium type. During dry years, water occurred in the lake during short-term rains and was evaporated after several days due to high temperature. This was observed in detail in August 2007, when water salinity increased from 43 to 260 g/L, while pH decreased from 9.5 to 7.99 during water evaporation, and bicarbonate concentration increased from 0.14 to 0.21 g/L. The results of hydrochemical analysis were published previously (Namsaraev et al., 2010).

Bottom sediments during the dry period. During the dry period, the lake was covered with a crust ~0.5 cm thick. At the crust surface, bloedite ($Na_2Mg(SO_4)_2 \cdot 4H_2O$) and halite (NaCl) crystals precipitated. Humidity of the crust was 4.7% (2007). The crust prevented water evaporation and drying of the bottom sediments. Water content in the sediments increased to 26.66% immediately below the crust (0.5–2 cm) and decreased to 11.83% in the 55–70-cm horizon. The pH of the water extract from the sediments decreased with depth from 8.6 (0–3 cm) to 8.13 (70 cm). In 2006–2007, excavation revealed pore water at the depth of 35–80 cm. Pore water salinity was 128–155 g/L, pH was 7.1–7.54.

The phototrophic community during the dry period. Microscopy of the crust at the bottom of dry lake revealed the high diversity of the cyanobacterial morphotypes (*Chroococcus minutus, Leptolyngbya tenuis, Leptolyngbya woronichinii, Coleofasciculus chthonoplastes,* and *Phormidium molle*) and green algae (*Oocistis* sp. and *Dunaliella salina*) in the upper, most dry layer of the crust (up to 1 mm thick). The subsurface crust layer (3–4 mm) was softer and often had purple coloration. In this layer, the number of anoxygenic phototrophic bacteria increased, which belonged to the families *Ectothiorhodospiraceae* (*Ectothiorhodospira* sp.), *Chromatiaceae* (*Marichromatium* sp., *Allochromatium* sp., *Marichromatium* sp.) and to the purple nonsulfur bacteria (*Rhodobacter* sp. and *Rhod-*

Table 1. Rates of production and terminal degradation processes in Lake Khilganta

Sample	Oxygenic photosynthesis	Anoxygenic photosynthesis	Dark CO_2 fixation	Sulfate reduction	Lithotrophic methanogenesis
	mg C /(dm^3 day)			mg S/(dm^3 day)	μL CH_4/(dm^3 day)
Crust above bottom sediments (2006)	1.5	2.3	0.68	15.93	230
Bottom sediments below the crust (2006)	N.D.	N.D.	0.24–1.082	0.4–2.2	20–379.5
Sample with *Dunaliella* sp. (2006)	0.877	0.029	0.034	N.D.	N.D.
Lake water (2007, S* 50 g/L)	3.28	0.27	N.D.	N.D.	N.D.
Cyanobacterial mat (2007, S 100 g/L)	18	16.6	8.2	2.87	29.3
Purple mat (2007, S 170 g/L)	13.1	60.6	59.8	N.D.	N.D.
Bottom sediments below thin mats at the rain period (2007, S 50 g/L)	N.D.	N.D.	0.7	48.05	576
Cyanobacterial mats, moist period (1999)	57.6	328.4	2.6	N.D.	N.D.
Bottom sediments below the cyanobacterial mat, moist period (1999)	N.D.	N.D.	N.D.	1.05–8.9	0.37–1.53

* S indicates total salinity. N.D. – no data.

ovulum sp.). The concentrations of chlorophyll *a* and bacteriochlorophyll *a* in the crust were 448 and 106 mg/m^2, respectively. Microscopy of the upper crust layer revealed the ratio close to ~1 : 1 for the numbers of empty sheaths of filamentous cyanobacteria to trichome-containing ones. The share of cyanobacterial sheaths with the cells decreased significantly with depth (to ~1 : 10 in the subsurface crust layer). This was probably an indication of more pronounced decomposition of cyanobacterial cells in deeper, more humid layers than at the surface.

During short-term rains of the dry period, the lake basin was filled with water for a short time. A thin film of a cyanobacterial mat developed on the lake bottom during 2–3 days, detached from the bottom, and floated to the surface due to oxygen bubbles forming inside the mat. The predominant cyanobacterial genus in the mat was *Geitlerinema*, while members of the genera *Nodularia* and *Oscillatoria* were also present. While the concentration of chlorophyll *a* in cyanobacterial mats was 61–89 mg/m^2, bacteriochlorophyll *a* content was below detection limit. After water evaporation for several days, salinity in the lake reached ~100 g/L, and cyanobacterial mats precipitated to the bottom and gradually decomposed. Within the salinity range of ~100–150 g/L, spots of purple bacteria emerged on the mat surface, in which *Ectothiorhodospira* sp. predominated. Both bacteriochlorophyll *a* (443 mg/m^2) and chlorophyll *a* (568 mg/m^2) were detected. At the final stage of drying (salinity of 200–260 g/L), pools remained in some depressions of the lake bottom, where green alga *Dunaliella salina* predominated, which is incapable of forming structured mats.

Rates of production processes. The rate of oxygenic photosynthesis in the mat crust (2006) was 1.5 mg C/(dm^3 day), while the rate of anoxygenic photosynthesis was 2.3 mg C/(dm^3 day). The rate of dark CO_2 fixation in the dry crust was 0.68 mg C/(dm^3 day).

The rate of oxygenic photosynthesis in the brine (2006), carried out mainly by *Dunaliella* sp., which predominated after evaporation of most water, was 0.877 mg C/(dm^3 day), while the rate of anoxygenic photosynthesis was lower, 0.029 mg C/(dm^3 day), and the rate of dark CO_2 fixation was 0.034 mg C/(dm^3 day).

During short-term rains of the dry period (2007), the lake basin was filled with water for sometime. In the water of the lake (2007, salinity 50 g/L, pH 9.03), the rates of oxygenic and anoxygenic photosynthesis were 3.28 and 0.27 mg C/(dm^3 day), respectively. Further water evaporation resulted in salinity reaching 100 g/L. The rates of oxygenic photosynthesis in cyanobacterial mats, anoxygenic photosynthesis, and

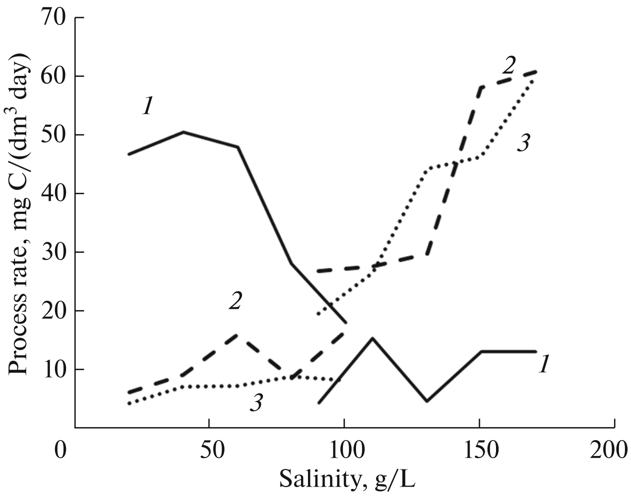

Fig. 1. Rates of production processes depending on salinity: oxygenic photosynthesis (*1*), anoxygenic photosynthesis (*2*), and dark CO_2 fixation (*3*). Cyanobacterial mat (graph with salinity values of 20—40—80—60—100 g/L) and purple mat (graphs with salinity values 90—110—130—150—170 g/L).

dark CO_2 fixation were 18, 16.6, and 8.2 mg C/(dm^3 day), respectively. When salinity increased to 170 g/L, the rate of oxygenic photosynthesis decreased to 13.1 mg C/(dm^3 day), while the rates of anoxygenic photosynthesis and dark CO_2 fixation increased sharply to 60.6 and 59.8 mg C/(dm^3 day), respectively. The rate of dark CO_2 fixation in the silt below the mat was 0.76 mg C/(dm^3 day).

The samples of cyanobacterial and purple mats collected at salinity of 100 and 170 g/L were incubated under conditions of different salinity. For this purpose, the brine from the lake was diluted with freshwater to desired salinity levels. Oxygenic photosynthesis was found to have a peak at 20–60 g/L salinity (46.6–50.4 mg C/(dm^3 day)). Salinity increase to 80 and 170 g/L resulted in the rate of oxygenic photosynthesis decreasing to 28 and 13.1 mg C/(dm^3 day), respectively. The trends for anoxygenic photosynthesis and dark CO_2 fixation were opposite. The rates of these processes were only 4.3–16 mg C/(dm^3 day) at 20–80 g/L, while at salinity of 170 g/L these processes became predominant with the rates of 60.6 and 59.8 mg C/(dm^3 day), respectively (Fig. 1).

Rates of the terminal decomposition processes. Microbial sulfate reduction was the dominant terminal decomposition process in the bottom sediments. The highest sulfate reduction rate was found in the crust, to 15.93 mg S/(dm^3 day), which corresponded to organic matter consumption of 11.95 mg C/(dm^3 day). In the crust, organic matter consumption via sulfate reduction exceeded the value for lithotrophic methanogenesis by two orders of magnitude.

Sulfate reduction was also the predominant decomposition process in the thin cyanobacterial mats developing during short-term rains. The rates of sulfate reduction and lithotrophic methanogenesis in the mat were 2.87 mg S/(dm^3 day) and 29.3 μL CH_4/(dm^3 day), respectively (salinity at the sampling time was 100 g/L). In the mats, organic matter consumption via sulfate reduction was two orders of magnitude higher than via methanogenesis, 2.11 and 0.06 mg C/(dm^3 day), respectively. The rates of the terminal processes of sulfate reduction and methanogenesis in the upper sediment layers below the cyanobacterial mat were 48.05 mg S/(dm^3 day) and 576 μL CH_4/(dm^3 day), respectively. Carbon consumption via sulfate reduction and methanogenesis was 36 and 1.2 mg C/(dm^3 day), respectively.

DISCUSSION

Our results made it possible to reconstruct successional changes of the functional activity of Lake Khilganta microbial community during the dry period. Evaporative concentration and increased water salinity after short-term rains resulted in changes of the types of microbial communities and the dominant pathways of carbon assimilation. After short-term rains in the dry period, the lake basin was filled with water with salinity ~30–50 g/L and pH ~9–9.5, and a thin cyanobacterial mat developed, in which filamentous cyanobacteria of the genus *Geitlerinema* predominated. The water gradually evaporated in the course of approximately 10 days, which resulted in its increasing salinity (Namsaraev et al., 2010). The highest rate of oxygenic photosynthesis, 18 mg C/(dm^3 day), was observed at 100 g/L salinity. Further increase in salinity resulted in development of red spots on the surface of the cyanobacterial mat; anoxygenic phototrophic bacteria of the genus *Ectothiorhodospira* predominated in these areas. The rate of oxygenic photosynthesis decreased, and anoxygenic photosynthesis and dark CO_2 fixation became predominant at the rates of 60.6 and 59.8 mg C/(dm^3 day), respectively. Their highest rates were observed at salinity ~170 g/L. Shifts in the dominant types of photosynthetic processes were accompanied by the changes in the ratio of chlorophyll *a* and bacteriochlorophyll *a* in microbial mats. Chlorophyll *a* predominated at 100 g/L salinity, while bacteriochlorophyll *a*, at 170 g/L. At ~200 g/L salinity the lake dried almost completely, with the water remaining the the surface only in isolated depressions, where salinity is 200–260 g/L and extremely halophilic eukaryotic microalga *Dunaliella* sp. predominated. Oxygenic photosynthesis was the dominant process at this stage, although its rate was relatively low, 0.877 mg C/(dm^3 day). Further evaporation resulted in formation of a dry crust, in which anoxygenic photosynthesis predominated at the rate of 2.3

mg C/(dm^3 day), which was somewhat higher than the rate of oxygenic photosynthesis.

Increased rates of microbial processes after short-term rains plays an important role in the functioning of the community, since significant amounts of organic matter are produced in the lake basin during this period. Oxygenic photosynthesis was the dominant process in the thin cyanobacterial mats formed after the rains, and the total production at this period exceeded the rates of terminal decomposition processes. Total production was 42.8 mg C/(dm^3 day), while carbon consumption via sulfate reduction and methanogenesis was 2.1 mg C/(dm^3 day). In the absence of rains, production processes were detected in the crust at the surface of the lake bottom, although their rates were an order of magnitude lower than the values for the rain period. Anoxygenic photosynthesis was the dominant process, as was indicated by the visually discernible purple layer below the crust. Total production was 4.5 mg C/(dm^3 day), while carbon consumption via the degradation processes was 12 mg C/(dm^3 day), indicating predominance of the degradation processes in the intervals between rainfalls.

The highest rates of photosynthetic production in Lake Khilganta during the moist period, 386 mg C/(dm^3 day) or 3.86 g C/(m^2 day) were two to three times lower than the values of 5–12 g C/(m^2 day) for Solar Lake in Egypt or those of up to 11 g C/(m^2 day) for the soda lakes of the East African rift zone (Melack and Kilham, 1974; Krumbein et al., 1977; Namsaraev et al., 2015). However, the rate of light-dependent CO_2 assimilation in Lake Khilngata mats and crusts was comparable to the rates of 0.15–0.29 g C/(m^2 day) reported for cyanobacterial and lichen crusts developing on soil in the Namib Desert and of up to 1 g C/(m^2 day) reported for the Central European steppe zone (Lange et al., 1994; Evans and Lange, 2001).

Sulfate reduction rate in Lake Khilganta was 0.4–48.05 mg S/(dm^3 day), which is comparable to the values of 0.128–13.5 mg S/(dm^3 day) reported for the bottom sediments of the Kulunda Steppe hypersaline alkaline lakes and is considerably higher than the maximal sulfate reduction rate of 0.073 mg S/(dm^3 day) revealed in the water column of the hypersaline alkaline Lake Mono (Oremland et al., 2004; Foti et al., 2007). The rate of lithotrophic methanogenesis in Lake Khilganta water and sediment samples was 0.37–576 μL CH_4/(dm^3 day), which was also comparable to the rates of 0.3–75.6 μL CH_4/(dm^3 day) reported for other saline and soda lakes in Mongolia and Transbaikalia (Namsaraev et al., 2015).

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