

EXPERIMENTAL
ARTICLES

Accumulation and Precipitation of Mn^{2+} by the Cells of *Oscillatoria terebriformis*

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Abstract—The cyanobacterium *Oscillatoria terebriformis* was shown to exhibit resistance to high manganese concentrations, remaining viable at 2.5 mM $MnCl_2$ in the medium. Cyanobacterial cells were capable of considerable manganese consumption from the medium. The dynamics of Mn sorption by the cells were the same in all experimental variants, independent of the manganese concentration. Manganese concentration in the biomass peaked after 2–3 days and depended on Mn^{2+} concentration in the medium and on the amount of biomass introduced. In the case of *O. terebriformis*, manganese removed from the medium may be subdivided into Mn absorbed by the cell, Mn bound to the cell wall, Mn absorbed by the glycocalyx, and chemically precipitated Mn. Of the total 21.25 ± 1.0 mg of consumed manganese, biological absorption and chemical precipitation were responsible for 11.78 ± 0.98 and 9.2 ± 0.8 mg, respectively. In the presence of cyanobacteria, Mn removal from the medium was 2.28 times higher than in the control. This process depended considerably on Mn sorption by exopolysaccharides. At 1.3 mM Mn^{2+} , a lamellar mat was formed with interlayers of manganese carbonate.

Keywords: cyanobacteria, manganese, consumption, precipitation, glycocalyx

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Manganese compounds are widespread in nature. Microorganisms play an active part in their formation and transformation [1]. In most rocks, Mn is present as a trace component. Manganese oxide may, however, occur in aggregates as sinters, lamellar concretions, and layers in stromatolites.

Genesis of the manganese-containing minerals has long been a subject of discussion. Formation of manganese-containing rocks and origin of Mn-containing stromatolites, however, still remain unclear and debatable. Detection of microfossils with lamellar localization indicates an active role of biological processes in formation of ferrimanganese concretions [2]. The oncolite–algal texture with selective separation of Fe and Mn in the Ushban horizon of the Malyi Karatau [3] also suggests involvement of microorganisms in the formation of manganese-containing stromatolites.

Manganese-oxidizing bacteria are diverse in their morphology and taxonomic position. Similar to the filamentous bacterium *Leptothrix*, they all possess a mucous capsule or sheath. In all cases, exocyttoplasmic biomineralization is the primary process. It includes enhanced mineralization in the presence of the mucous extracellular polysaccharides, which is followed by the crystalline or amorphous mineral filling the capsule or sheath.

All of these bacteria are organotrophic. Recent investigation of the manganese-oxidizing bacteria from deep-water hydrotherms revealed, however, that some of them were autotrophic microorganisms [1].

The Mn^{+2} ion is the form of manganese most easily available to bacterial cells. Its concentrations in the ecosystems are, however, extremely low. Efficient systems for its absorption are therefore necessary, especially if an organism has a specific manganese requirement. Such organisms include cyanobacteria, which incorporate manganese in their oxygen-evolving complex [4]. Indirect Mn^{+2} oxidation not involving enzymes has been studied only for the unicellular cyanobacterium *Microcystis* and for the unicellular green alga *Chlorella* [5]. In both cases, oxidation was carried out under illumination and was coupled to photosynthesis, which saturated the medium with oxygen and increased its pH to 10.

Intense development of cyanobacteria resulting in oxygen accumulation in the atmosphere required protection from the oxidative stress. Oxygenic photosynthesis results in oxygen reduction to the anionic superoxide radical, which is converted to H_2O_2 . Mn^{+2} , which reacts with hydrogen peroxide, therefore became required for the preservation of the viability of microbial cells under oxidative conditions [5]. The

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role of cyanobacteria in manganese turnover in nature is therefore significant.

Manganese ions are transported into a cyanobacterial cell by the ABC type transporter, which is encoded by the *mnt-CAB* operon [6]. The latter is actively expressed at low levels of Mn (e.g., in seawater). This system regulates manganese accumulation under limiting conditions and enables the cells to achieve the Mn concentration required for their metabolism. While expression of the operon is inhibited at high manganese concentrations, manganese may accumulate to high concentrations, up to those lethal to cyanobacteria. Elevated Mn concentrations are known to inhibit protein synthesis [7]. Marine microorganisms, which have adapted to low-manganese environments, have limited abilities to develop the mechanisms preventing manganese transport inside the cell.

Resistance of cyanobacteria to manganese depends, apart from environmental factors and the culture age, on the presence of specific and nonspecific protective mechanisms [8–10]. Nonspecific resistance is associated with manganese detoxification in the medium or at the cell surface prior to its penetration into the cell. Cell envelopes and extracellular metabolites, especially carbohydrates, are responsible for this activity [9]. Various proteins binding significant amounts of manganese in the cytoplasm are responsible for specific resistance [10]. Thus, the cell both prevents manganese intake and requires it, since this element is a necessary component of many enzymes.

The presence of diverse mechanisms of the interaction between cyanobacterial cells and manganese, as well as the ancient origin of these organisms, which were predominant at the time of stromatolite formation, suggest investigation of their role in manganese precipitation and in formation of Mn-containing stromatolites.

In the present work, in order to simulate the conditions favorable for formation of Mn-containing cyanobacterial mats (modern analogues of stromatolites), the effect of MnCl_2 on the growth of *Oscillatoria terebriformis* was studied, as well as the capacity of its cells for fossilization and manganese accumulation.

MATERIALS AND METHODS

The subject of research was the algologically pure culture of *Oscillatoria terebriformis* from the cyanobacterial collection of the Laboratory of Relict Microbial Communities, Winogradsky Institute of Microbiology, Russian Academy of Sciences (INMI). The organism was isolated from a cyanobacterial mat of the Ter-mal'nyi hydrothermal spring (Uzon caldera, Kamchatka, Russia). This organism was chosen for investigation, since in its natural habitats it grows under conditions of continuous manganese influx and is able to

accumulate up to 0.4% intracellular Mn (wt/wt for absolutely dry biomass) [11].

Cyanobacteria were grown in Zavarzin medium [12], simulating the water composition of a hydrothermal spring and containing $1.8 \mu\text{M}$ Mn, under sterile conditions and 24-h illumination (2000 lx) at 30°C . For determination of the effect of manganese on cyanobacterial growth, the standard Zavarzin medium was supplemented with 0.25, 0.5, 1.3, 2.5, 5.0, 25, or 50 mM MnCl_2 , added at the time of inoculation. In the control variants, Mn was not further added to the medium. Manganese accumulation by cyanobacterial cells was determined at two MnCl_2 concentrations (0.25 and 1.3 mM). Since [13] reported dependence between Mn accumulation by bacterial cells and the amount of biomass inoculated, two experimental series were carried out. In the first one, cyanobacterial biomass grown in the optimal medium was collected on a plankton net, washed three times with water, ground in a mortar to obtain a homogeneous suspension, and used to inoculate the petri dishes (5 mL per 20 mL of the medium, initial biomass 13.7 mg). For the second series, the cyanobacterial film grown in the dishes was transferred to conical flasks with 500 mL of fresh medium and specified MnCl_2 concentrations (initial biomass 237 mg).

Biomass accumulation was monitored as weight of the absolutely dry biomass (adb). For this purpose, the mass of adsorbed manganese was subtracted from the mass of dry matter.

Manganese content in the culture medium and in *O. terebriformis* biomass incinerated by the wet process in a mixture of nitric and perchloric acids [8] was determined on a Hitachi 270 atomic absorption spectrophotometer (Japan) in the Dokuchaev Soil Institute, Russian Academy of Agricultural Sciences.

Cyanobacterial morphology and the elemental composition of the formed minerals were determined in the Borisyak Paleontological Institute, Russian Academy of Sciences (PIN) on scanning electron microscopes CamScan-4 (Cambridge) and EVO50 XVP (Zeiss, Germany) equipped with an INCA Oxford 350 microanalyzer.

Statistical treatment of the results. The experiments were carried in three biological repeats and in at least three analytical ones. The results of typical experiments and the relative standard errors are presented.

RESULTS

Cyanobacterial growth at different MnCl_2 concentrations. The cells of *O. terebriformis* were resistant to high manganese concentrations (Fig. 1) and remained viable at 2.5 mM MnCl_2 . Variation in behavior of the cultures supplemented with different MnCl_2 concentrations were observed after day 7 of cultivation. While in the control culture the cyanobacterial film spread over all the area of the vial, 0.25 mM MnCl_2 caused

inhibition of cyanobacterial growth, which resulted in a visibly decreased biomass increment and contraction of the biofilm. At 0.5 mM MnCl₂, the biofilm was also lumpy, and a manganese carbonate precipitate was formed at the bottom of the vial. At 1.3 mM, the lag phase duration increased and the growth rate was several times lower than in the control. While cyanobacterial growth was completely inhibited at 2.5 mM, the cells retained chlorophyll; a green film of cyanobacterial filaments and manganese carbonate was formed at the bottom of the vial. Some cells remained viable, and growth was resumed after 30 days, when chemical precipitation resulted in a decrease in Mn concentration. A green film of growing cyanobacteria was formed at the water surface. Cyanobacteria did not survive MnCl₂ concentrations of 5 mM and higher, and a brown precipitate was formed, consisting of magnesium carbonate and cyanobacterial detrital biomass.

Morphology of cyanobacteria at different MnCl₂ concentrations. Microscopy of cyanobacteria grown at different manganese concentrations revealed that growth inhibition was accompanied by alterations in cell morphology (Fig. 2). The state of the culture in the presence of Mn is summarized in the table.

Formation of mineralized cyanobacterial filaments, with some cells preserving their viability, was observed at 1.3 mM MnCl₂. For our purposes (to obtain significant mineralization of the trichomes under conditions of growth, albeit somewhat suppressed), this concentration was optimal. The state of

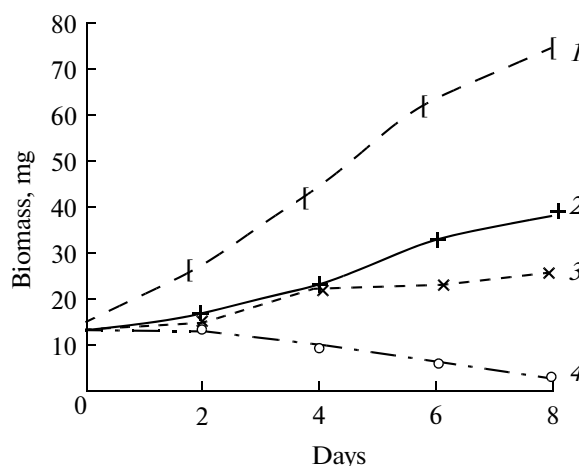


Fig. 1. Biomass of the cyanobacterium *O. terebriformis* grown in media with different Mn concentrations: control, 1.8 μM (1); 0.25 mM (2); 1.3 mM (3); and 2.5 mM (4).

the culture after 9 and 75 days of growth in the medium with Mn is shown on Fig. 3. After 9 days, only fossilized cyanobacterial filaments were found in the precipitate (Fig. 3a), while after 75 days live cyanobacterial filaments with the gliding motion typical of *O. terebriformis* were present (Fig. 3b). The cyanobacterial biofilm had a pronounced lamellar structure (Figs. 3c, 3d). Alternating mineral and cyanobacterial layers were well discernable in the forming mat.

Effect of different MnCl₂ concentrations on cell morphology and mineralization

Mn concentration, mM	Culture description
0.25	Filaments covered with a thin mucous film, which is normally not present in <i>Oscillatoria</i> (Fig. 2a). Below the film, trichomes with thin, barrel-shaped cells are visible (Fig. 2b)
0.5	Mucous sheaths become thick, obscuring the trichome morphology (Fig. 2c)
1.0	Numerous empty sheaths twisted ribbonlike (Fig. 2d). Trichomes with and without sheaths. Mn is present (Fig. 7)
1.3	Live trichomes form local zones on the film surface. Numerous MnCO ₃ globules appear (Fig. 8). Among the mineralized glycolyx, fossilized filaments are present (Fig. 2e)
2.5	Trichomes with and without mucous sheaths among the globules and detritus mass. Filaments with mucous sheaths do not reveal individual cells. Numerous mineralized sheaths and trichomes (Fig. 2f), live cells are extremely rare
5	Abundant Mn-containing organic matter and mucus. Dead mineralized cyanobacterial filaments among MnCO ₃ globules (Fig. 2g). The histogram (Fig. 8) confirms the mineral composition of these globules and the absence of organic components
10–25	Precipitate of MnCO ₃ globules and mucus-covered, deformed trichomes. Among the mineralized detritus and mineral globules, decayed cyanobacterial filaments occur (Fig. 2h). The mineral formed is rhodochrosite (MnCO ₃ · nH ₂ O). No live filaments are present

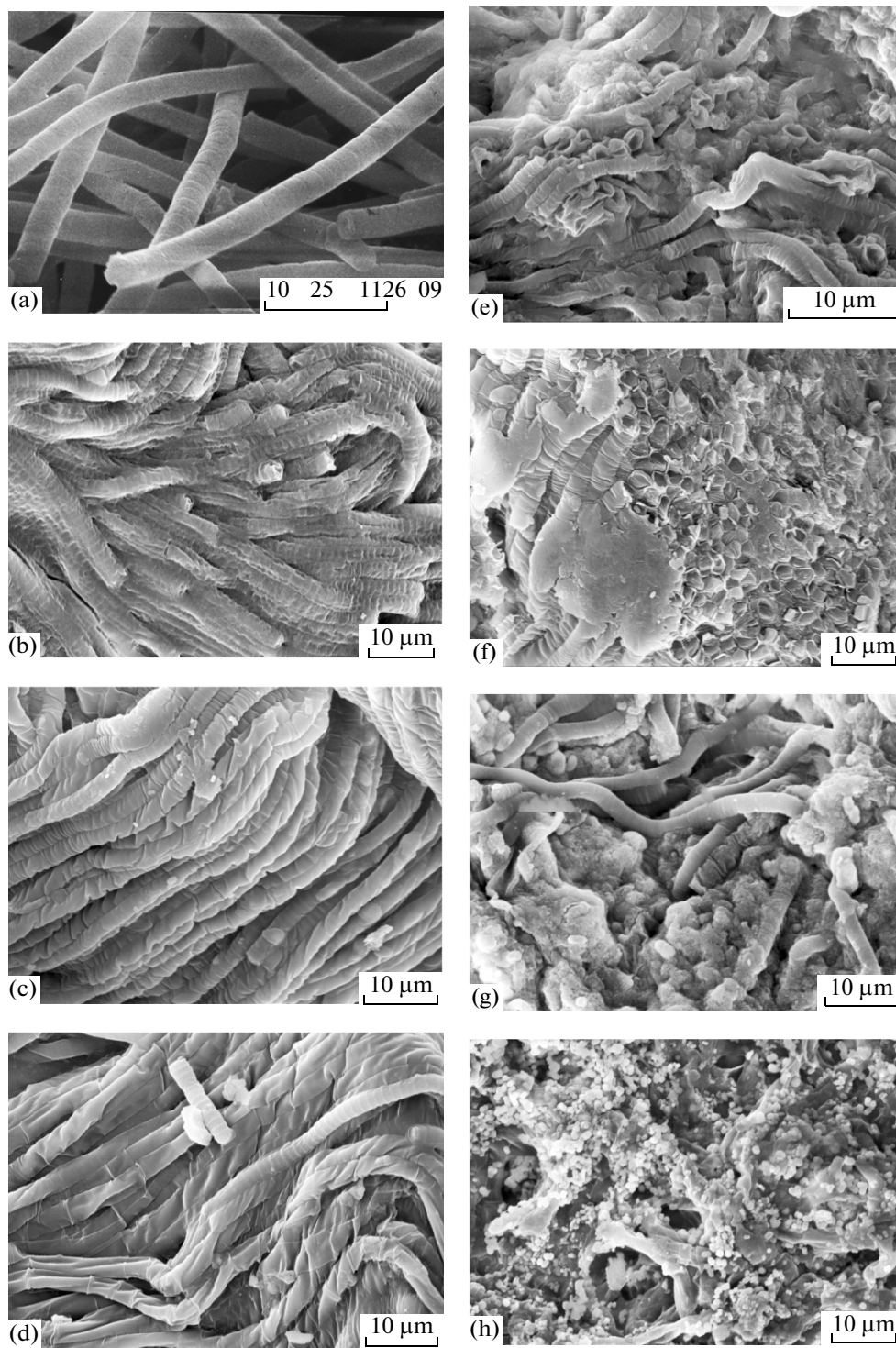


Fig. 2. Morphology of *O. terebriformis* in the presence of different MnCl_2 concentrations: control, 1.8 μM (trichomes with thin, barrel-shaped cells without sheaths) (a); 0.25 mM (formation of thin mucous sheaths) (b); 0.5 mM (formation of thick sheaths) (c); 1.0 mM (twisted deformed filaments in sheaths) (d); 1.3 mM (mineralized glycoalkalix, trichomes are living the mineralized sheaths) (e); 2.5 mM (mineralized trichomes and sheaths with a trichome crawling out of the detritus) (f); 5.0 mM (mineral MnCO_3 globules, mineralized filaments, and live trichomes) (g); and 10.0 mM (mineralized cyanobacterial filaments embedded in mineral precipitate) (h).

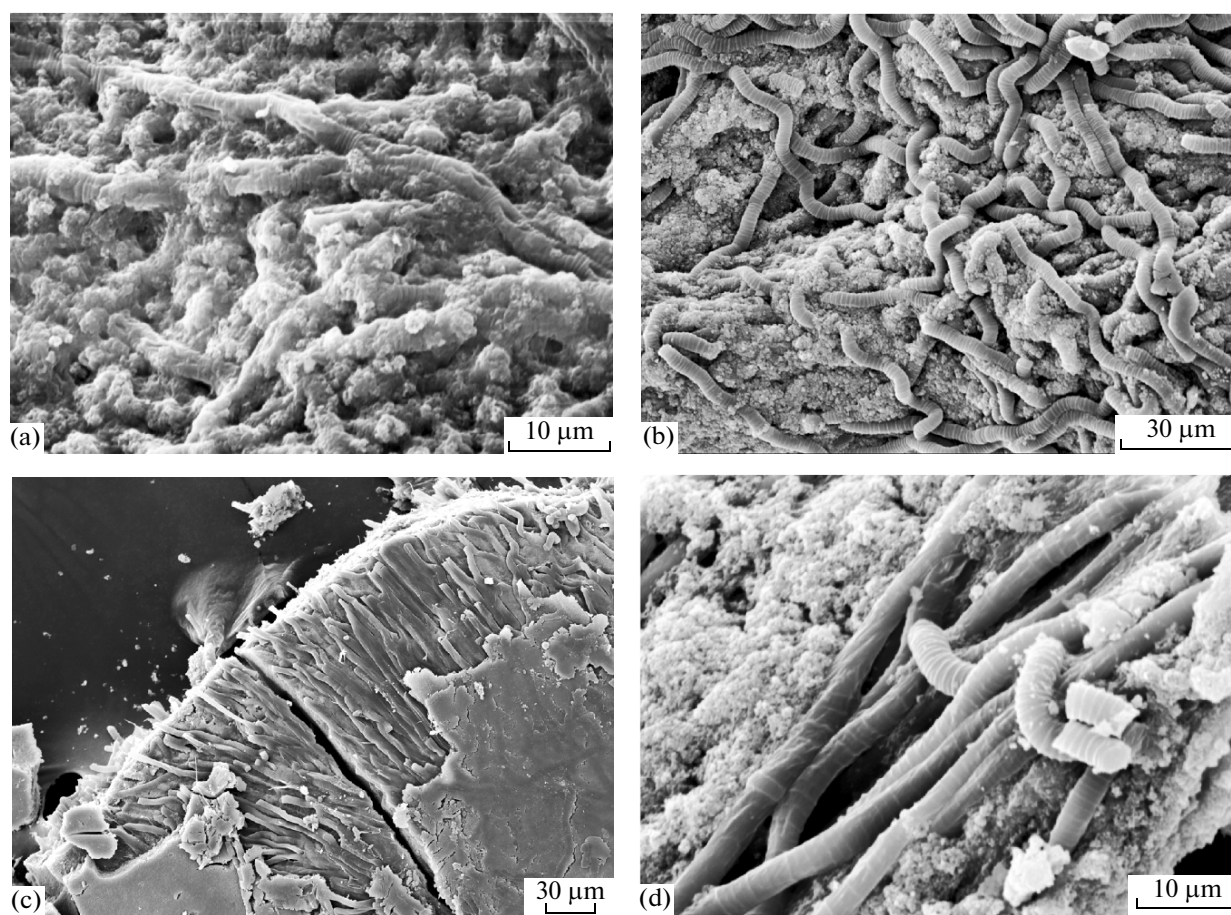


Fig. 3. Formation of a stratified cyano-bacterial mat with $MnCO_3$ by *O. terebriformis* grown in the medium with 1.3 mM Mn: mineral precipitate with mineralized trichomes on day 9 (a), live trichomes in the sediment after 2.5 months (b), and a laminated cyano-bacterial mat formed after 1 month (c, d).

Dynamics of Mn accumulation by the cells. Manganese accumulation by *O. terebriformis* cells was proportional to the cultivation time and Mn concentration in the medium (Fig. 4). At all manganese concentrations, the dynamics of its absorption by the cells was the same in all experimental variants. At 0.25 mM, all Mn was consumed by the cells and no chemical precipitation occurred (Fig. 5). Initially, its concentration in the biomass increased tenfold and then began to decrease, since cyanobacterial growth continued, while all manganese was already removed from the medium. At 1.3 mM, the highest manganese level in the cells was 34 ± 0.1 mg/g adb on day 2 and subsequently decreased, in spite of significant residual manganese concentration in the medium (Fig. 6). An insignificant increase in the manganese concentration in the medium on day 3 probably indicated desorption.

Thus, at all Mn concentrations in the medium, its maximal accumulation by cyanobacterial cells occurred after 48 h. In the case of increased inocula, however, Mn concentration in the biomass reached 32.5 ± 0.7 mg/g adb on day 2 and continued to

increase to 44.75 ± 4.3 mg/g adb on day 3 (Fig. 4). This may result from the formation of high amounts of extracellular polysaccharides, which adsorb much more manganese than the trichomes themselves (Figs. 7, 8). According to [14], at elevated manganese concentration, the polysaccharides of *Gloeotheca magna*, a cyanobacterium with well-developed mucous sheaths, could absorb up to 906 mg/g absolutely dry mucous mass.

Figs. 5 and 6 show that the timeline of Mn removal from the medium was a mirror image of the curve of Mn accumulation in the biomass. The total amount of manganese accumulated in the biomass was, however, lower than the amount removed from the medium (Fig. 9). At 1.3 mM Mn it was to some degree precipitated chemically, as was confirmed by chemical analysis (Figs. 6, 9) and microscopy (Fig. 2h).

DISCUSSION

Our experiment showed that the thermophilic culture of *O. terebriformis* was able to consume significant amounts of manganese from the medium. The highest

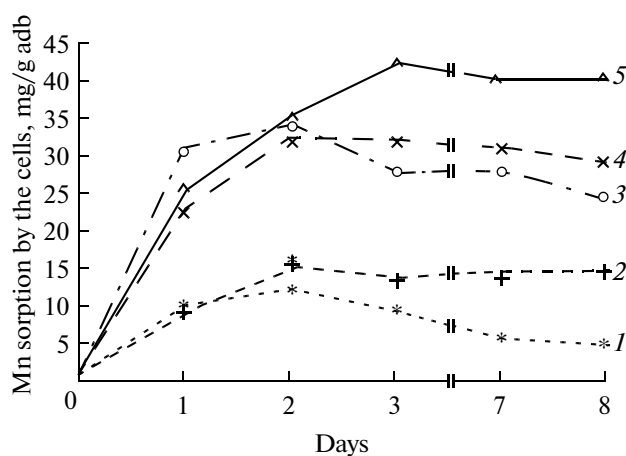


Fig. 4. Mn sorption by *O. terebriformis* depending on the initial MnCl_2 concentration in the medium: 1.8 μM (1), 0.25 mM (2), 1.3 mM Mn (3 and 5), and 2.5 mM (4), as well as on the amount of cyanobacterial inoculum: 13.7 mg adb (1, 2, 3, 4) and 237 mg adb (5).

levels of manganese accumulation in the biomass were achieved during the first two to three days and depended on manganese concentration in the medium and on the introduced amount of biomass. The saturation limit was observed at 2.5 mM manganese in the medium.

The few works on quantitative assessment of manganese consumption by bacterial and cyanobacterial cells yielded diverse results. For example, the cyanobacterium *Spirulina platensis*, which is highly resistant to manganese, were found to grow, albeit very slowly, in the presence of 5.1 mM MnCl_2 in the medium [10]. Manganese accumulation by *S. platensis* cells (up to $28 \pm 3 \mu\text{mol/g}$ dry mass) was proportional to the cul-

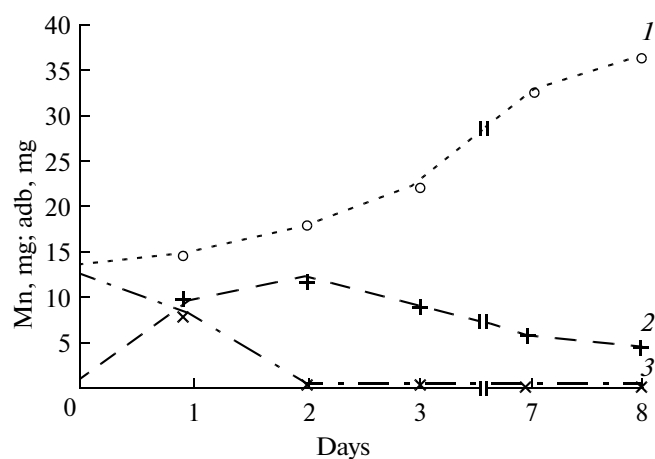


Fig. 5. Mn consumption by *O. terebriformis* from the medium with initial Mn^{2+} concentration of 0.25 mM: growth curve, mg adb (1); intracellular accumulation, mg Mn/g adb (2); and removal from the medium, mg Mn/L (3).

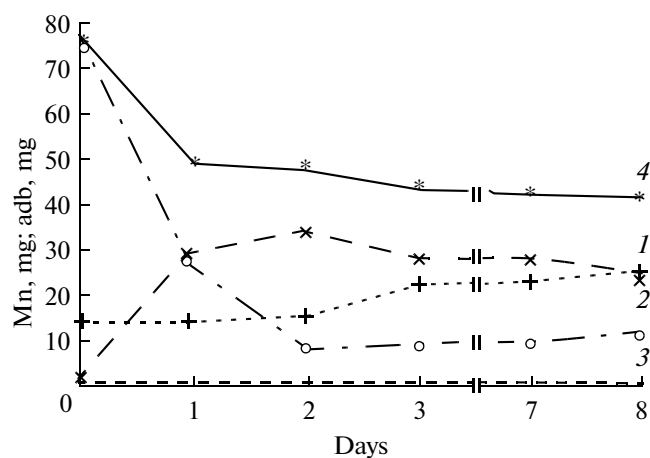


Fig. 6. Mn consumption by *O. terebriformis* from the medium with initial Mn^{2+} concentration of 1.3 mM: growth curve, mg adb (1); intracellular accumulation, mg Mn/g adb (2); removal from the medium in the presence of *O. terebriformis*, mg Mn/L (3), and removal from the medium by chemical precipitation without cyanobacteria, mg Mn/L (4).

tivation time and manganese concentration, with saturation at 2.5 mM Mn in the medium. For bacteria isolated from water treatment facilities, manganese accumulation was shown to depend on experimental conditions (pH and concentrations of Mn and the biomass). Optimization of the cultivation conditions resulted in biosorption increasing from 13.31 to 55.56 mg/g biomass [13]. For a mixture of algae and cyanobacteria isolated from a blooming water reservoir in one of the Chinese provinces, manganese concentrations above 0.13 mM were shown to result in growth arrest followed by cell death [15]. In our experiments, the increment of cyanobacterial biomass on day 7 was in the presence of 0.25 mM Mn was half that of the control. While *O. terebriformis* was more sensitive to Mn than *S. platensis*, dying off at 5 mM Mn, manganese accumulation in its biomass was more than ten times higher than in *S. platensis*. This may be due to several reasons. First, unlike *S. platensis*, *O. terebriformis* was isolated from a thermophilic mat of a hydrothermal spring with a constant Mn influx, where mat-forming cyanobacteria accumulated 2.1 to 4.2 mg Mn/g dry mass [11]. Moreover, while cyanobacteria developing in a mat produce abundant mucous polysaccharides, which were shown to sorb up to 904 Mn/g dry mass [14], this is not the case for *Spirulina*.

According to Baker's classification of plants and microorganisms by their ability to accumulate heavy metals [16], *O. terebriformis* belongs to manganese hyperaccumulators. The threshold manganese accumulation by hyperaccumulator algae *Kirchneriella* sp. (*Selenastraceae*, *Chlorophyta*) and by plant cells (*Apoynaceae*, *Celastraceae*, *Chusiaceae*, *Myrtaceae*, and

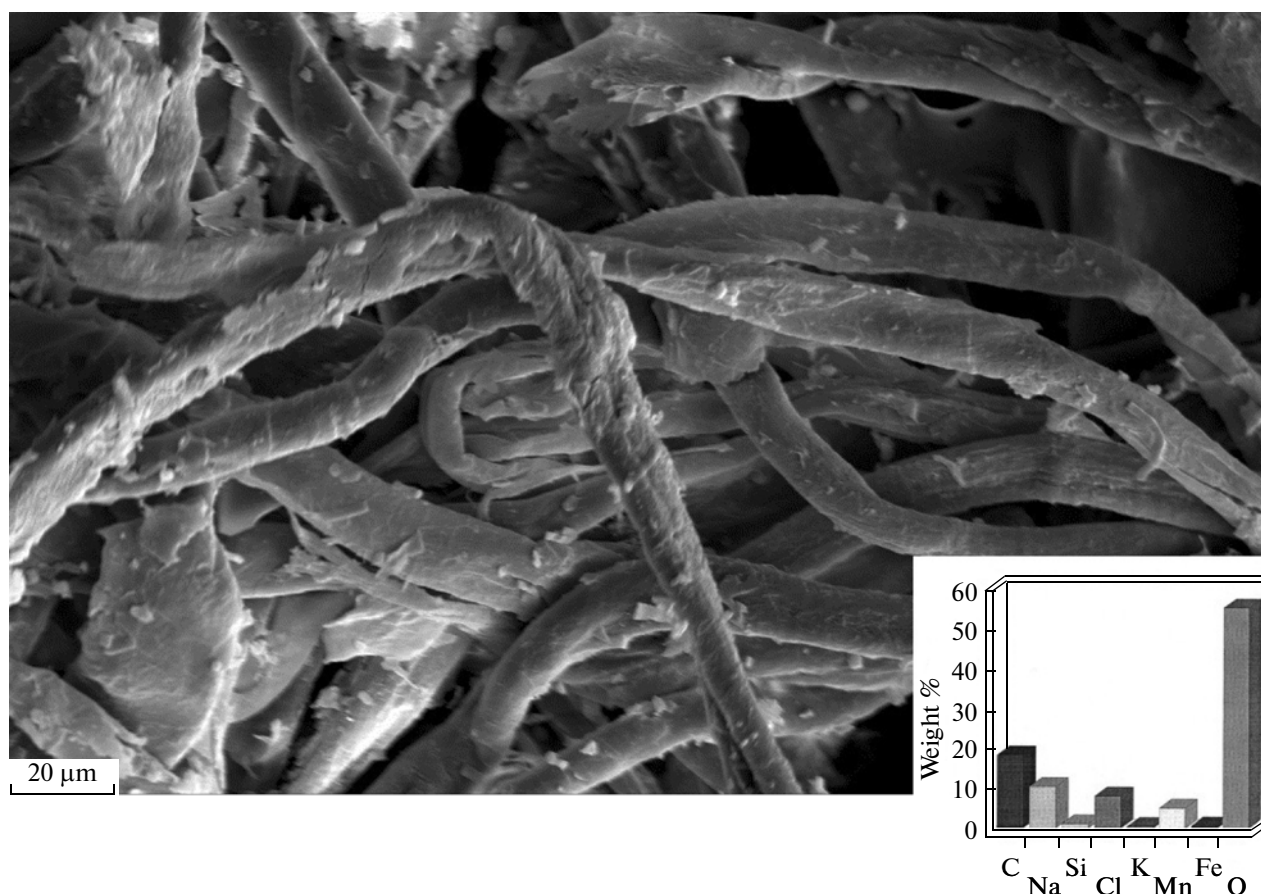


Fig. 7. Morphology and elemental composition of cyanobacterial filaments determined on an INCA-350 microanalyzer at 1.3 mM MnCl₂ in the culture medium (experimental duration, 9 days).

Proteaceae) were about 10 and 18 mg/g dry mass, respectively [17]. The value for *O. terebriformis* was four times higher than the threshold for algae and 2.5 times higher than in plant cells.

For *O. terebriformis* cells grown in the medium with 1.3 mM Mn, (268.2 ± 2.16 mg adb, 500 mL of the medium), all Mn removed from the medium fell into the following groups: (1) Mn sorbed by the cell; (2) Mn bound to the cell wall; (3) Mn sorbed by the glycocalyx, and (4) chemically precipitated Mn. Of the total amount of manganese removed (21.25 ± 1.0 mg), biological absorption and chemical precipitation were responsible for 11.78 ± 0.98 and 9.2 ± 0.8 mg, respectively (Fig. 9). Removal of manganese from the medium in the presence of cyanobacteria was 2.28 times higher than in the control (Figs. 6, 9). This process depended significantly on manganese sorption by exopolysaccharides (Figs. 7, 8).

Thus, a nonspecific protective mechanism (Mn binding by exopolysaccharides) plays the major role in *O. terebriformis* growing at high manganese concentrations in the medium. Formation of large amounts of mucus is a natural function of cyanobacteria in

cyanobacterial communities, which is responsible for the preservation of the structure of the mat. Excretion of these extracellular metabolites is known to increase in the presence of metals [10], which is the factor responsible for binding significant amounts of manganese.

Our results demonstrated that *O. terebriformis* is able to absorb significant amounts of soluble manganese compounds (MnCl₂) and to precipitate insoluble ones (MnCO₃) on the filaments and in the glycocalyx. These data, together with the ancient origin of cyanobacteria and their predominance in the Precambrian stromatolites, suggest the possible involvement of cyanobacteria in formation of Mn-containing stromatolites in the geological past.

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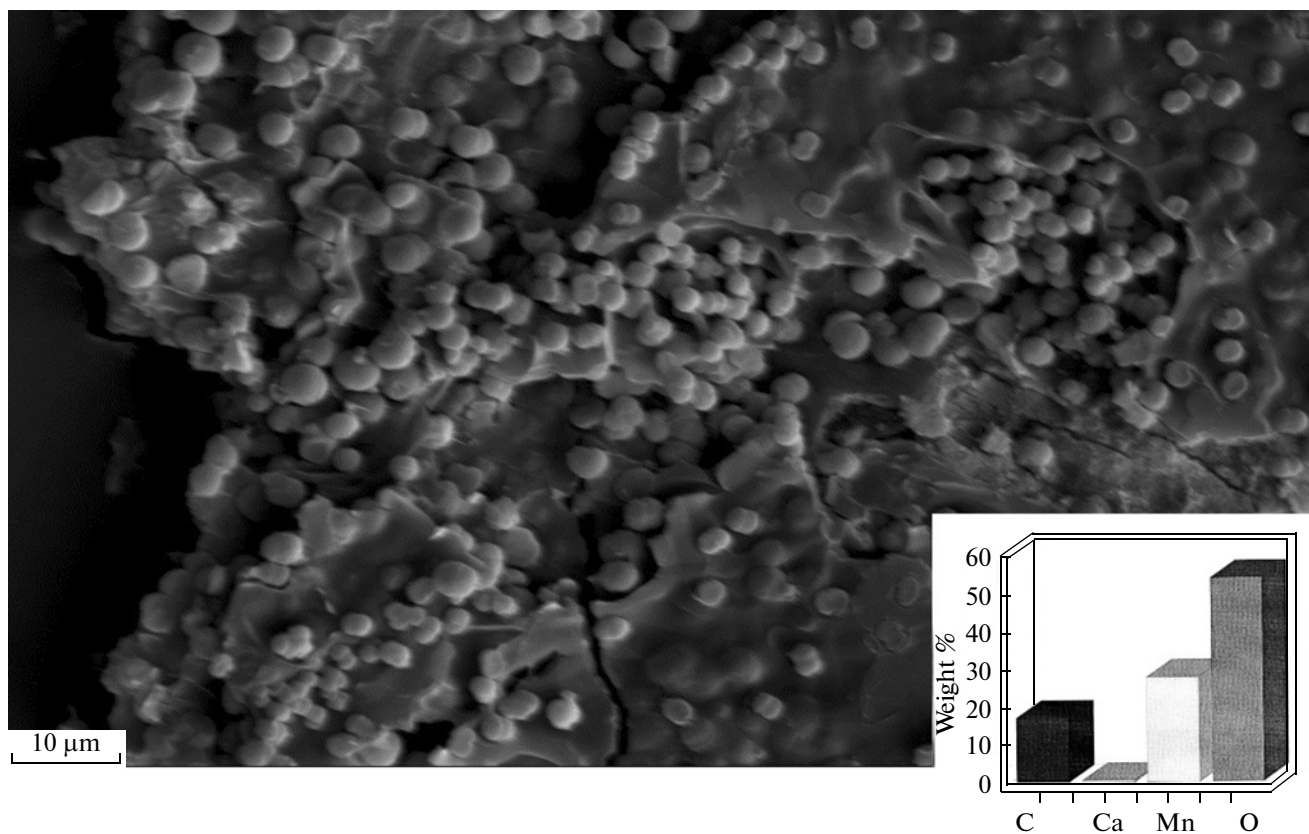


Fig. 8. Formation of mineral globules on the glycocalyx and their elemental composition determined on an INCA-350 microanalyzer at 5 mM MnCl_2 in the culture medium (experimental duration, 9 days).

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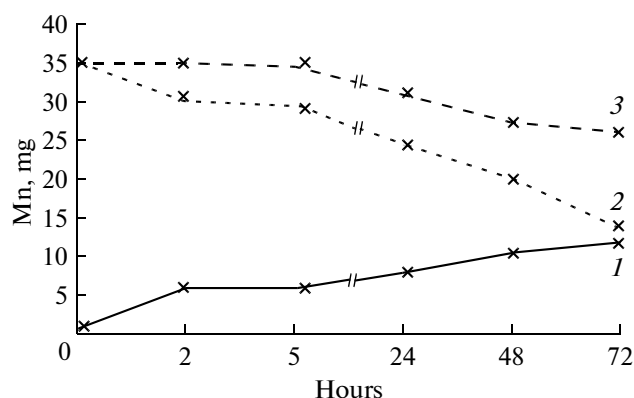


Fig. 9. Mn dynamics in bacterial biomass, culture medium, and chemical precipitate at the initial Mn concentration 1.3 mM: total Mn in cyanobacterial biomass, mg Mn per 268.2 mg dry biomass (1); Mn removed from the medium by cyanobacteria, mg Mn per 500 mL of the medium (2); and chemically precipitated Mn in the medium without cyanobacteria, mg Mn (3).

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