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Fungi Inhabiting the Coastal Zone of Lake Magadi

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Abstract—Fungi able to survive under the extreme environment of soda lakes remain poorly studied. This paper presents data on the diversity and ecophysiology of filamentous fungi inhabiting one of the most alkaline habitats of the Earth: Lake Magadi, where pH values may exceed 11–12. The lake is home to a large number of prokaryotes, which form complex communities with algae and some other eukaryotes. In this study, 22 species of filamentous fungi isolated from soil samples collected on the coastline of Lake Magadi have been characterized using a systematic approach, which includes selective isolation, an analysis of morphological traits, molecular–genetic analysis, growth experiments to determine pH and temperature preferences, and an analysis of the dependence on NaCl concentrations. According to the results, alkaline soil from the Lake Magadi coastline is colonized by fungi with differing types of adaptation to high pH values. Alkaliphilic and alkalitolerant fungi belong to different families of Ascomycetes, mainly to Plectosphaerellaceae, as well as to Onygenaceae, Trihocomaceae, and Pleosporaceae. *Sodiomyces tronii* and *S. magadii* are new obligate alkaliphilic species within the earlier monotypic genus *Sodiomyces* (Plectosphaerellaceae). According to the growth experiments, obligate alkaliphilic isolates demonstrate thermo- and halotolerant properties. The problems of adaptation to the external pH, possible substrate preferences, and association of alkaliphilic fungi with other organisms are discussed.

Keywords: extremophiles, alkaliphilic fungi, alkalotolerant fungi, thermotolerant fungi, *Sodiomyces*, soda lakes, Lake Magadi

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INTRODUCTION

Soda lake Magadi is situated in the southern part of the Great Rift Valley in Kenya (Eastern Africa). The area of this lake is about 100 km^2 (Matagi, 2004). Lake Magadi has the highest mineralization level among the lakes of the Great Rift Valley and is one of the most alkaline habitats on the Earth; pH values for this lake reach 10–12 (Grant, 2006). Such stably soda lakes and alkali soils are common in arid and semiarid zones. Intensive water evaporation and leaching of surrounding rocks deficient in Ca^{2+} and Mg^{2+} lead to the formation of concentrated carbonate-bicarbonate brines with high pH values and high buffer capacity (Grant, 2006). The climatic zone of Lake Magadi is characterized by the alternation of rainy and drought seasons; during droughts, the lake is almost completely covered by a white soda layer, and the day temperature may exceed 40°C (Matagi, 2004; Muruga and Anyango, 2013). The alteration of wet and dry periods provides regular salinity drops. The lake salinity may vary from 0.1‰ (feed water) to >300‰ (Jones et al., 1977).

Despite such extreme conditions, soda lakes are considered among the most productive water habitats (Melack and Kilham, 1974; Oduor and Schagerl, 2007). The basic primary producers of moderately saline lakes located near Lake Magadi in the Great Rift Valley are *Arthrospira* spp. and other cyanobacteria. This habitat is characterized by a succession of primary producers; unlike most other soda lakes, algal mats in these lakes are formed by cyanobacteria in lake lagoons only during rainy seasons (Jones et al., 1998; Muruga and Anyango, 2013; Krienitz and Schagerl, 2016). It seems that anoxygenic phototrophic halophilic bacteria *Ectothiorhodospira* also play an important role in primary production (Matagi, 2004; Grant, 2006). Eukariots such as diatomic and green algae also contribute to the primary production (Matagi, 2004).

High primary production causes mass flocks of birds, especially the lesser flamingo *Phoeniconaias minor*, which come to the Lake Magadi to feed during the intensive development of the lake microflora (Jones et al., 1998; Grant, 2006). Among other vertebrates inhabiting the lake, one should mention the unique tilapia fish (*Oreochromis alcalicus*) adapted to the extreme alkaline conditions (Kavembe et al., 2016). Unfortunately, there is no reliable data on the invertebrates of Lake Magadi. As far as we know, there are no publications indicating the presence of brine shrimps (*Artemia salina*) inhabiting many other soda lakes (Cole and Brown, 1967). The lake flora is represented by both herbaceous (*Cynodon dactylon* (L.) Pers., *Dactyloctenium* sp., etc.), and tree (*Acacia*, etc.) forms. Interestingly, there is no mention on saltworts from the family Chenopodiaceae, which are common for such biotopes.

The diversity of prokaryotic communities of soda lakes is well-studied, and the presence of all main trophic groups able to form all basic biogeochemical closed cycles has been shown (Zavarzin et al., 1999; Grant and Jones, 2016). On the contrary, the diversity of eukaryotes was always considered to be very low. However, the application of molecular genetic methods has shown a tremendous hidden diversity of microscopic eukaryots in soda lakes, and their trophic relationships were found to be much more complex than has been considered earlier (Luo et al., 2013; Schagerl and Renaut, 2016). Fungi, known as important destructors in many ecosystems, are poorly studied in the Lake Magadi habitat. Studies of fungi, which have proven their ability to grow under alkaline–saline conditions, have recently began on the lake coasts and saline lands of the Kulundinskaya steppe, Transbaikalia, the Gobi Desert, and Tanzania (Bilanenko and Georgieva, 2005; Bilanenko et al., 2005; Georgieva et al., 2012a, 2012b; Grum-Grzhimaylo et al., 2013a, 2013b). According to the published data, these ecosystems are inhabited by alkalitolerant fungi, which prefer neutral pH values, and alkaliphilic fungi (facultative and obligate), for which high pH values are optimal (Grum-Grzhimaylo et al., 2016).

As for Lake Magadi, the study of its coastal soils by culturing methods (Salano, 2011) and the study of its hot springs by high-throughput sequencing (Kambura et al., 2016) have revealed fungi, many of which are known as eurybionts or neutrophils. At the same time, there is no data on their ability to not only survive, but also develop under alkaline conditions. This study is an evaluation of the functional diversity of fungi living under strong alkaline conditions of Lake Magadi performed by a combination of traditional and selective methods of isolation, morphological and phylogenetic analysis, and growth experiments for the physiological characterization of isolates.

MATERIALS AND METHODS

Samples

Samples were collected in January 2013 on the coast of Lake Magadi (Kenya). The top 5-cm layer of soil was collected along the coastline. There were ten sampling sites for eastern (S01.54133°, E36.17888°) and western (S01.52461°, E36.16027°) coasts each. On the eastern coast, samples were collected near the water edge (0.5–1 m) 2–3 m far from the vegetation. On the western coast, soil samples were collected in the flooded zone located along the soda-covered dried part of the lake; in this part of the coast there was no vegetation. Soil pH and humidity were determined for all samples.

Isolation and Culture Media

The selective isolation of alkalitolerant fungi and their further culturing were carried out using an alkaline agar (AA, pH 10.2) prepared from the wort and carbonate-bicarbonate buffer (Bilanenko and Georgieva, 2005; Grum-Grzhimaylo et al., 2013a). Wort agar (WA, pH 6.5) was chosen as a standard medium with neutral pH suitable for the isolation and culturing of micromycetes. Bacterial growth on AA was inhibited by rifampicin (2 g/L), which was the most efficient antibiotic among 21 preparations tested on this medium (Grum-Grzhimaylo et al., 2016). In the case of WA, bacterial growth was inhibited by the addition of lactic acid (4 mL/L).

Isolation Techniques

Inoculation was performed using a soil-lump technique, i.e., via the distribution of soil lumps on the surface of Petri plates filled with AA. In the case of WA, inoculation was carried out either by the soil lump technique or by the use of a diluted soil suspension (1 g of soil per 10 mL of water). Inoculated plates were wrapped in Parafilm and incubated at room temperature.

To quantify the presence of fungi in soil samples, the number of grown colonies was calculated and then the number of colony-forming units (CFUs) per 1 g of dry soil was determined. The frequency of each fungal species was calculated as the ratio of the number of samples containing this species to the total number of samples (%).

For all isolated fungi, their monosporous isolates were obtained and included into the Collection of Extremophilic Fungi of the Department of Mycology and Algology of Moscow State University. Some isolates were also deposited into the VKM-Russian Collection of Microorganisms (Pushchino, Russia) and the CBS culture collection (Utrecht, Netherlands).

Morphological Identification of Isolates

The identification of micromycetes isolated into a pure culture was carried out using identification guides and contemporary papers on fungal taxonomy (Raper and Fennell, 1965; Raper et al., 1968; Gams, 1971; Domsch et al., 2007; Zare et al., 2007; Bensch et al., 2010; Hirooka et al., 2014, etc.). Names and systematic positions of fungi are given in accordance with the Index Fungorum database (http://www.indexfungorum.org). The study and illustration of fungal micromorphology was carried out using light (LM), scanning electron (SEM), and low-temperature scanning (cryo-SEM) microscopy.

Molecular Identification of Isolates

DNA isolation, amplification, and sequencing were carried out at the Laboratory of Genetics of the Wageningen University (Netherlands). Isolates were identified via the sequencing of different gene loci, such as the internal transcribed spacer region (ITS rDNA), actin (Act), β-tubulin (β-tub), calmodulin (CMD), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), RNA polymerase II large subunit (RPB2), and transcription elongation factor 1α (TEF-1α) (Table 1). DNA extraction, amplification, and sequencing were carried out as described earlier (Grum-Grzhimaylo et al., 2016); in the case of AcT, β-tub, and CMD, procedures corresponded to those described by Bensch et al. (2010) and Visagie et al. (2014). The taxonomic identification of species was carried out using a BLAST program (GeneBank); for some isolates, additional phylogenetic analysis was performed using Bayesian analysis and the maximum-likelihood method (Bondarenko et al., 2016).

Study of Physiological Properties of Isolates

The character of adaptation of fungi to alkaline conditions was determined using an earlier developed procedure, namely, the measurement of a linear fungal growth in tubes filled with media differing in their pH (Grum-Grzhimaylo et al., 2016). Fore these experiments, we used WA-based media, the pH of which was stabilized by the addition of 0.2 M citrate (pH 4.5), 0.2 M phosphate (pH 7), and 0.2 M carbonate-bicarbonate (pH 9 or 10) buffers. Cultures were incubated in the dark under controlled temperature conditions (28°C).

For some isolates, their temperature tolerance and resistance to NaCl in the nutrient medium were determined within the range of 15–50°C and 0–2 M NaCl, respectively, via the evaluation of a culture growth on Petri plates under optimal pH conditions (Bondarenko et al., 2017). *Sodiomyces alkalinus* isolates were obtained from the collection of extremophilic fungi of the Department of Mycology and Algology of Moscow State University.

Table 1. Gene loci used for the molecular identification of isolates

Group of fungi	Gene loci
Alternaria	ITS, LSU, GAPDH
Aspergillus	ITS, LSU, β-tub, CMD, RPB2
Chrysosporium	ITS, LSU
Cladosporium	ITS, LSU, Act, TEF-1α
Fomitopsis	ITS, LSU, TEF-1α, RPB2
Gibellulopsis	ITS, LSU, TEF-1α
Hydropisphaera	ITS, LSU
Hypocreales sp.	ITS, LSU
Irpex	ITS, LSU
Mycelia sterilia (Mag4 isolate)	LSU, β-tub, RPB2
Penicillium	ITS, LSU, β-tub, CMD, RPB2
Peniophora	ITS, LSU, TEF-1α
Phlebia	ITS, LSU
Pleosporales sp.	ITS, LSU, TEF-1α, GAPDH, RPB2
Sodiomyces	ITS, LSU
Talaromyces	ITS, LSU, β-tub, CMD, RPB2

Table 2. Species composition and frequency of micromycetes isolated on alkaline nutrient agar from the alkaline soil of the Lake Magadi coastline

Taxon	Frequency, %
ASCOMYCOTA	
Dothideomycetes	
Pleosporales, Pleosporaceae	
Pleosporales sp.	5
Eurotiomycetes	
Eurotiales, Trichocomaceae	
Aspergillus ustus (Bainier) Thom et Church	5
Onygenales, Onygenaceae	
Chrysosporium lobatum Scharapov	5
Sordariomycetes	
Glomerellales, Plectosphaerellaceae	
Sodiomyces tronii sp.nov.	10
Sodiomyces magadii sp.nov.	5
Gibellulopsis nigrescens (Pethybr.) Zare, W. Gams et Summerb.	10
INSERTAE SEDIS	
Mycelia sterilia (isolate Mag4)	5

RESULTS

The soil of sampling sites was characterized by an extreme degree of alkalization: pH values of collected samples varied within the range of 10.5–10.8 with a mean value of 10.7 ± 0.1. Despite the use of antibiotics, a large number of bacteria (actinomycetes and various *Bacillus* species) were isolated on WA. Fungal species were revealed in 16 out of 20 samples; 1 g of dry soil contained ~120 CFU on average, while there was only 1 CFU/g in the case of AA usage. The frequency of some species did not exceed 5–10%. In total, the use of two types of agar medium resulted in the isolation of 22 micromycete species from 20 samples of alkaline soil (Tables 2, 3).

All fungi isolated on AA belonged to the Division Ascomycota (six species) and represented mainly the family Plectosphaerellaceae, as well as several single species from the families Trichocomaceae, Onygenaceae, and Pleosporales (Table 2). Two new species of the obligately alkaliphilic genus *Sodiomyces* have been described, illustrated, and published in our earlier

Table 3. Species composition and frequency of micromycetes isolated on wort agar from the alkaline soil of the Lake Magadi coastline

Taxon	Frequency, %
ASCOMYCOTA	
Dothideomycetes	
Capnodiales, Cladosporiaceae	
Cladosporium cladosporioides complex*	10
Cladosporium sphaerospermum complex*	5
Pleosporales, Pleosporaceae	
Alternaria sect. *Alternata**	5
Eurotiomycetes	
Eurotiales, Trichocomaceae	
*Aspergillus creber** Jurjevic, S.W. Peterson et B.W. Horn	5
Aspergillus sect. *Nigri**	5
Paecilomyces variotii Bainier	5
*Penicillium solitum** Westling	5
*Penicillium commune** Thom	10
*Penicillium multicolor** Grig.-Man. et Porad.	10
*Penicillium herquei** Bainier et Sartory	10
Talaromyces sect. *Islandici**	5
BASIDIOMYCOTA	
Agaricomycetes	
Polyporales, Fomitopsidaceae	
*Fomitopsis pinicola** (Sw.) P. Karst.	5
Polyporales, Meruliaceae	
*Irpex lacteus** (Fr.) Fr.	10
Phlebia sp.*	5
Russulales, Peniophoraceae	
Peniophora sp.*	5

study and included *Sodiomyces tronii* Bondarenko, A.A. Grum-Grzhim., A.J.M. Debets et Bilanenko and *Sodiomyces magadii* Bondarenko, A.A. Grum-Grzhim., A.J.M. Debets et Bilanenko (Grum-Grzhimaylo et al., 2016). Note that isolates of these two species were revealed either on the eastern (*S. tronii*) or western (*S. magadii*) coasts of Lake Magadi. The taxonomic position of one sterile isolate (Mag4) still remained unclear. Attempts to stimulate asexual or sexual sporulation on 16 media with different pH levels were unsuccessful. Molecular genetic methods did not assist in the identification of this fungus either, since we did not succeed in sequencing the ITS region. Sequences of other loci indicated that this fungus seems to belong to the Division Ascomycota.

Inoculation on standard neutral WA medium showed soil samples contained fungi from both Ascomycota and Basidiomycota. Ascomycetes were represented by 11 species from the families Trichocomaceae and Cladosporiaceae, as well as the Order *Pleosporales*. According to the molecular genetic analysis, almost all sterile isolates belonged to four species of basidial fungi from the Orders Polyporales and Russulales (Table 3).

Physiological Characterization of Fungi of Lake Magadi

Growth-tube experiments showed that fungi inhabiting alkaline soils of the Lake Magadi coastline are characterized by different types of pH adaptation.

Obligate alkaliphiles (isolates of new *Sodiomyces* species and a sterile Mag4 isolate with unclear taxonomy) preferred alkaline conditions and were unable to growth on media with pH < 5 (Fig. 1). In contrast to obligate alkaliphiles, a facultative alkaliphile *Chrysosporium lobatum* was able to grow under acidic conditions (Fig. 2). Species with moderate (*Aspergillus ustus*, *Pleosporales* sp.) and strong (*Gibellulopsis nigrescens*) alkalitolerance preferred neutral pH, but were able to develop even at higher pH (Fig. 2).

Fungi isolated on WA included only weakly alkalitolerant species and species unable to grow under alkaline conditions (Fig. 3). The first group included *Aspergillus* sect. *Nigri*, *Paecilomyces variotii*, *Penicillium herquei*, *P. multicolor*, and *Irpex lacteus*. The second group consisted of *Fomitopsis pinicola*, *Peniophora* sp., *Phlebia* sp., and *Talaromyces* sect. *Islandici*.

A study of the temperature dependence of the growth rate of *S. magadii* and *S. tronii* was carried out in comparison with *S. alkalinus* isolates collected from alkaline soils in different regions of Russia, Mongolia, and Tanzania. According to the data on the growth rates of *S. tronii* and *S. magadii* measured on AA at 15–50°C, these fungi were able to grow at a wider temperature range than *S. alkalinus* isolates, such as typical F11, F16, and F10 isolates from Mongolia, Kulunda Steppe, and Tanania, respectively (Fig. 4). *S. magadii* and *S. tronii* were able to grow at 40°C, whereas no *S. alkalinus* isolates (the authors did not show data on other isolates) were able to develop under such conditions. The optimum growth temperature for *S. tronii* and *S. magadii* was 32°C, while all *S. alkalinus* preferred 28°C. Thus, according to the character of their adaptation to temperature, *S. magadii* and *S. tronii* were considered thermotolerant species.

A study of the dependence of the growth rate on a NaCl concentration under optimal pH values showed that both *S. tronii* and *S. magadii* grew better on a NaCl-free medium, but they were able to develop even if the NaCl concentration reached 2 M (Fig. 5). Thus, these species may be considered halotolerant.

DISCUSSION

The number of fungal germs in the alkaline soil samples from Lake Magadi was very low and varied

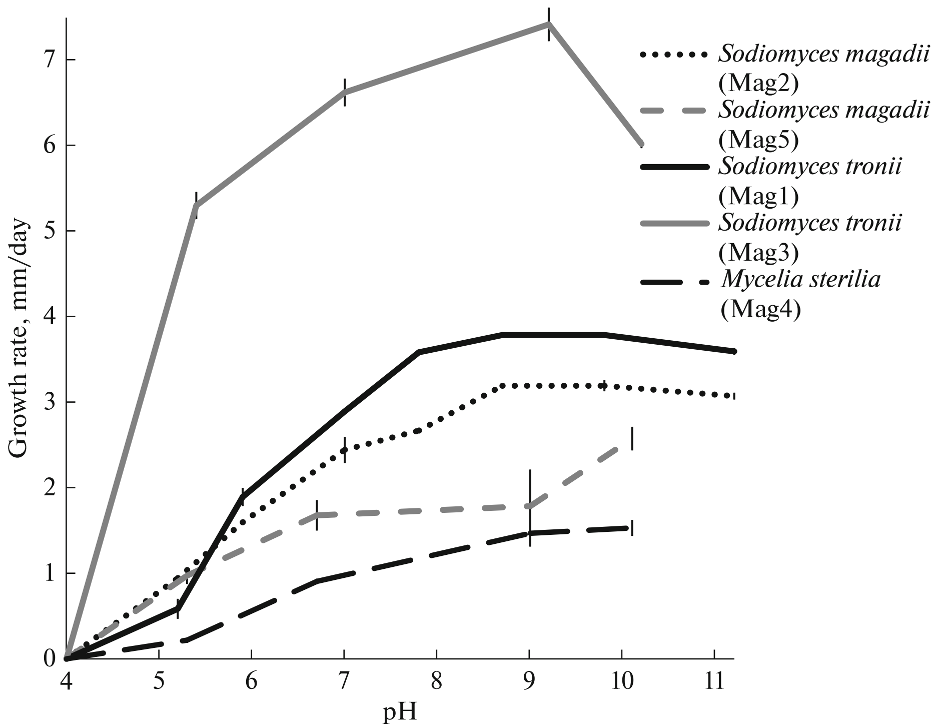

Fig. 1. Dependence of the linear growth rate of fungi, isolated on an alkaline agar from the soil of the Lake Magadi coastline, on the pH of nutrient medium.

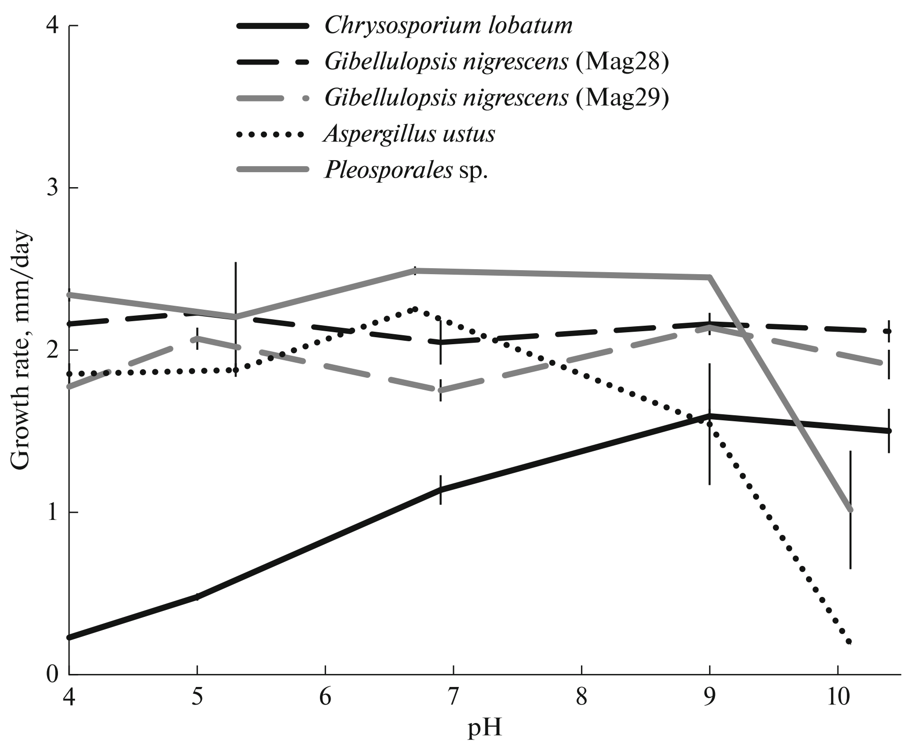

Fig. 2. Dependence of the linear growth rate of fungi, isolated on an alkaline agar from the soil of the Lake Magadi coastline, on the pH of nutrient medium.

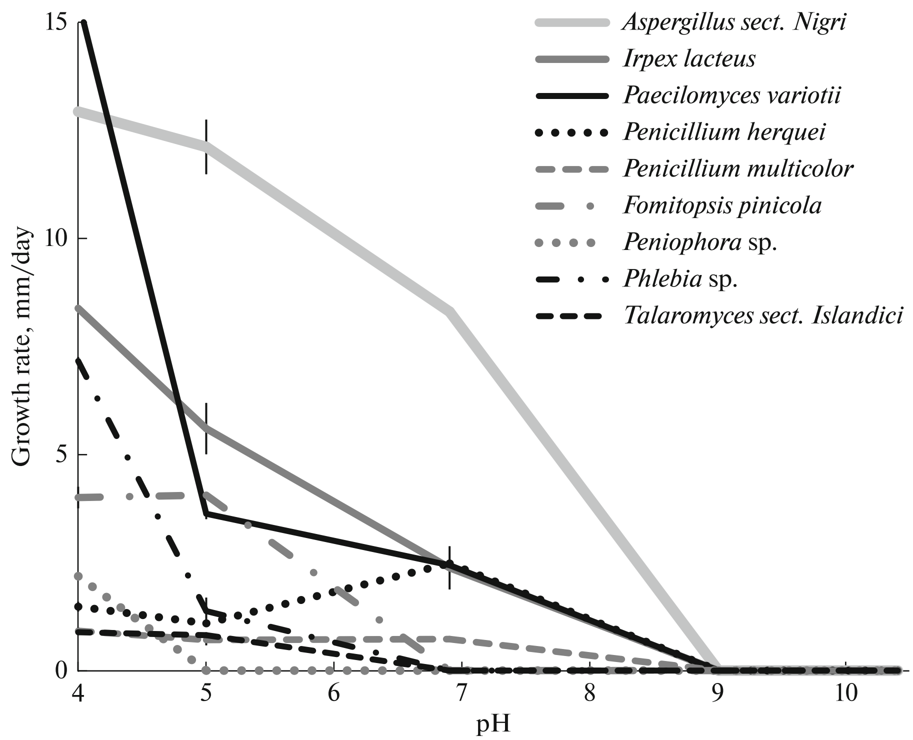

Fig. 3. Dependence of the linear growth rate of fungi, isolated on a wort agar from the soil of the Lake Magadi coastline, on the pH of nutrient medium.

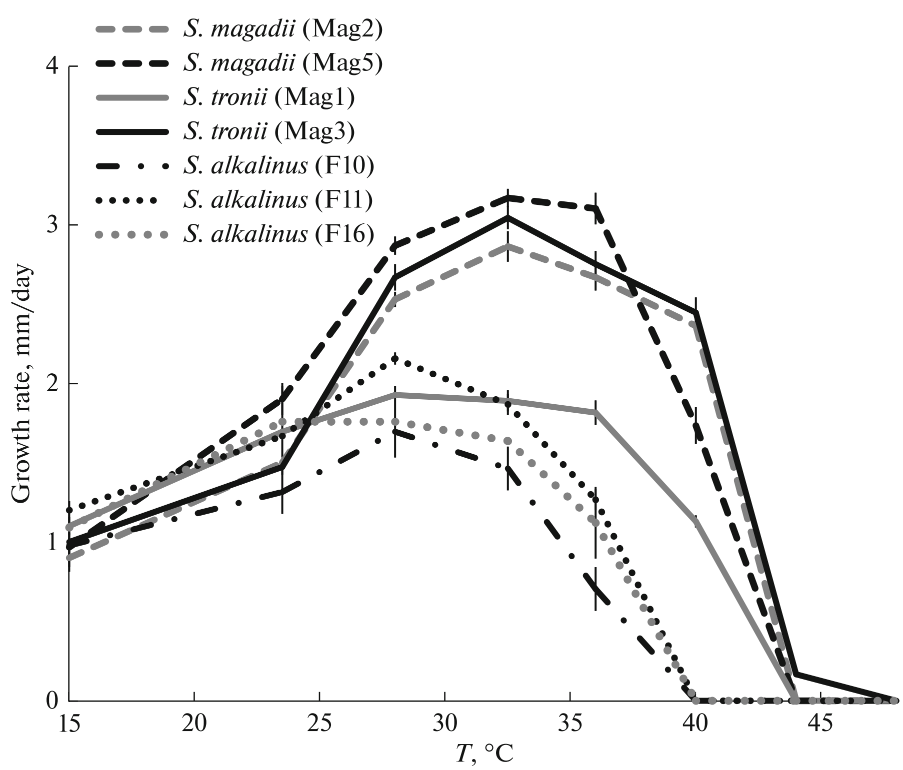

Fig. 4. Temperature dependence of the growth rate of some alkaliphilic isolates from the genus *Sodiomyces*.

from zero to several CFU/g for AA medium and from zero to 10^2 CFU/g for the WA medium, which is several orders lower than the values known for neutral soils (Ozerskaya, 1980; Mirchink, 1988). The frequencies of separate species in the alkaline soil were also rather low and did not exceed 5–10%.

All alkaliphilic and alkalitolerant species isolated on the WA medium belonged to ascomycetes and included species of the family Plectosphaerellaceae and single species from the families Trichocomaceae, Onygenaceae, and Pleosporales. The taxonomic position of one isolate (*Mycelia sterilia* Mag4) remained unknown. It seems this fungus also belongs to the Division Ascomycota. Such taxonomic distribution, i.e., the presence of only ascomycetes, mainly from the family Plectosphaerellaceae, is typical for the alkalitolerant part of soda lake communities (Grum-Grzhimaylo et al., 2016).

The obligate alkaliphilia of fungi from the genus *Sodiomyces* was confirmed by the example of two new species revealed on the lake coast. *S. magadii* formed closed ascocarps with developing two-cell ascospores, but it did not generate a conidial stage. *S. tronii* developed in the form of asexual stage generating well-developed conidiophores; in the case of sexual-stage development, the fungus formed ascocarps, but did not produce ascospores (Fig. 6). *S. alkalinus*, which is common for stably alkaline habitats of Western Siberia, Russia, Mongolia, and Tanzania, usually demonstrates holomorphic growth in culture and generates asexual and sexual sporulation. It was proposed to consider this species an indicator of stable alkaline salinization (Grum-Grzhimaylo et al., 2013a, 2016). Another obligate alkaliphile is *Mycelia sterilia* Mag4, a fungus with an unclear taxonomic position; the culture of this fungus was characterized by a light sterile mycelium.

The analyzed samples also contained facultative alkalifilic fungi (*Chrysosporium* sp.), as well as strong (*Gibellulopsis nigrescens*) and moderate (*Aspergillus ustus*, *Pleosporales* sp.) alkalitolerant fungi, whose relation to alkaline habitats has been revealed earlier. For example, alkalitolerant fungi *Aspergillus ustus* and *Gibellulopsis nigrescens* from the order Pleosporales have been found earlier in soda saline lands (Grum-Grzhimaylo et al., 2016), species from the genus *Chrysosporium* were isolated from Japan limestones (pH 7.8–8.8; Nagai et al., 1998), and *Gibellulopsis nigrescens* was also isolated on an alkaline medium from neutral and acid soils (Bondarenko et al., 2016).

The isolation of fungi from alkaline soils of the Lake Magadi coastline using standard neutral WA medium allowed us to reveal fungal species from the divisions Ascomycota and Basidiomycota and, at the same time, a complete absence of zygomycetes, whose high frequency and diversity is typical for other soil types. All isolated fungi were either unable to grow under alkaline conditions (the majority of Basidiomycetes), or sharply reduced their growth rate at pH 6.5–7.0 and did not develop at pH 9 (most fungi from the families Cladosporiaceae, Pleosporaceae, and Trichocomaceae). The largest part of these ascomycetes (*Cladosporium cladosporioides*, *Alternaria* sect. *Alternata*, *Aspergillus* sect. *Nigri*, *Penicillium* spp., etc.) are known to be widespread in various habitats around the world. Germs of these fungal species detected by standard techniques simply occur in the alkaline soil but did not function under such conditions.

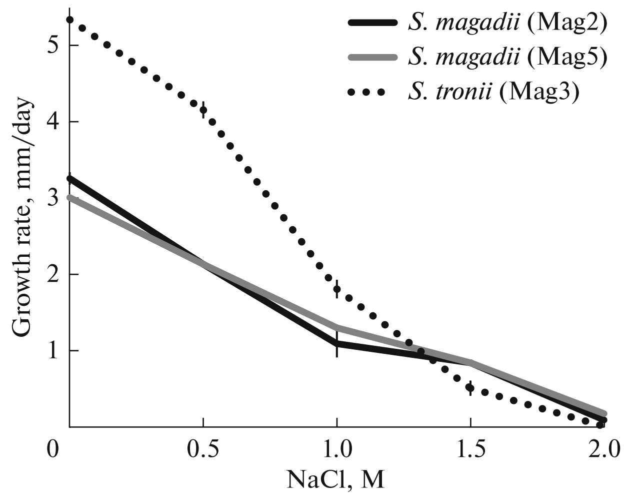

Fig. 5. Dependence of the growth rate of some alkaliphilic isolates on the NaCl concentration in a nutrient medium.

What is the role of alkalitolerant fungi in Lake Magadi? A large amount of organic debris is accumulated in the water and on the coastline of this lake; they include products of a bird activity, remains of invertebrates, dying cells of photosynthesizing microorganisms, etc. In many habitats, fungi are known as basic destructors of complex organic substrates. Alkalitolerant species may play this role in soda lakes. In addition, they may be associated with plants growing along the lake coastline. Such a connection with plants was established for *Gibellulopsis nigrescens* and *Pleosporales* sp., which were also revealed in the studied samples (Domsch et al., 2007).

The ecological niche of obligate alkaliphiles from the genus *Sodiomyces* is unclear. Physiological studies demonstrate that these fungi are well-adapted to the extreme conditions of Lake Magadi. Along with the obvious growth optimum in the alkaline pH range, new *Sodiomyces* species isolated from the soil samples collected from the Lake Magadi coastline are characterized by a high thermotolerance: these fungi have a heightened temperature optimum and are able to grow even at 40°C. For all revealed *Sodiomyces* fungi, optimal NaCl concentrations vary between 0 and 0.1 M, while the growth of fungi was observed even at 2 M of NaCl. In the case of *S. tronii*, such a dependence was shown earlier in relation to other pH values using

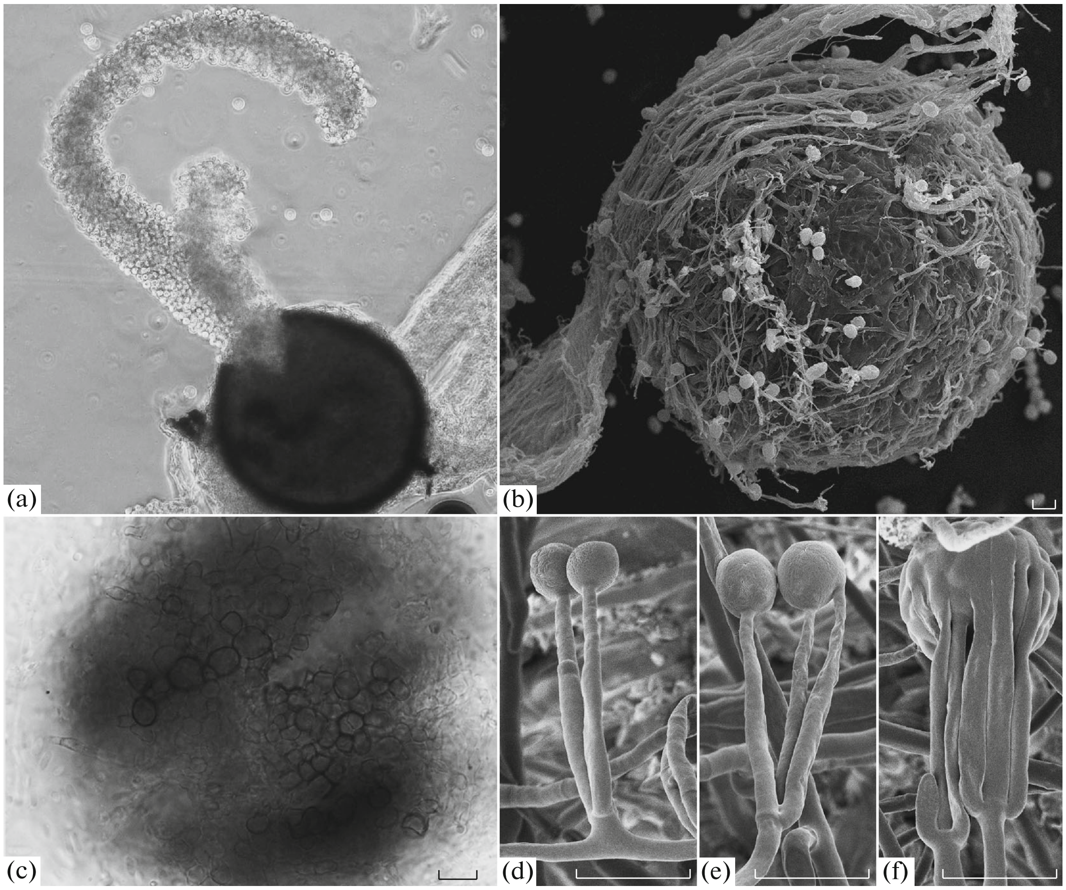

Fig. 6. *Sodiomyces magadii*: (a) exit of slime and ascospores from the ascocarp (light microscopy); (b) ascocarp (scanning electron microscopy). *Sodiomyces tronii*: (c) early stage of the ascocarp formation. Chains of chlamydospores participating in the formation of exoperidium; (d–f) Conidiophores with conidium heads in a slime (low-temperature scanning microscopy). The scale bar is 10 μm for all pictures.

media based on other buffer systems. It was also shown that the increase in the molarity of an alkaline carbonate-bicarbonate buffer results in a decreased growth of the fungi, which, however, continues even if the molarity reaches 0.7 (Bondarenko et al., 2017). It seems the *Sodiomyces* species are able to resist strong mineralization, but grow only during wet periods, when the level of a lake mineralization decreases. This hypothesis is confirmed by the morphological characteristics of these fungi. Closed ascocarps and abundant slime formation around the mycelium and sexual or asexual spores (Fig. 6) probably allow the fungi to survive during drought and strong mineralization periods; at the same time, their spores are probably spread in a humid environment.

The adaptation of *S. tronii* and *S. magadii* to extreme conditions is confirmed by their biochemical features. These alkaliphiles are characterized by the unique composition of soluble cytosolic carbohydrates; particularly, by an increased content of trehalose, maintained even in the case of variations of external pH (Bondarenko et al., 2017, 2018).

It is known that the obligate alkaliphile *Sodiomyces alkalinus* prefers complex carbon sources, especially under alkaline conditions (Grum-Grzhimaylo et al., 2013a). It is possible that *Sodiomyces* species may be associated with bacteria. The fungus is always isolated from soil together with bacteria living in the slime surrounding its mycelium. A pure culture of this fungus can be obtained only by a series of passages on an antibiotic-containing medium. Another evidence of a possible association with prokaryots is the presence of bacterial genes in the genome of *Sodiomyces alkalinus* (Grum-Grzhimaylo, 2015). Therefore, *Sodiomyces* species inhabiting alkaline habitats may also develop together with bacteria forming biofilms or biocrusts.

CONCLUSIONS

The occurrence of fungi with different levels of adaptation to extreme environmental conditions (pH > 10, high salinity, and temperature drops) on the coast of Lake Magadi has been experimentally confirmed for the first time. The amount of such fungi in the soil is rather low. Along with viable germs of fungi able to persist, but not develop, under such conditions (ascomycetes *Aspergillus*, *Penicillium*, *Talaromyces*, and *Paecilomyces*; basidiomycetes *Fomitopsis*, *Phlebia*, *Irpex*, and *Peniophora*), we revealed species resistant to the abovementioned stress factors: haloalkalitolerant (*Aspergillus ustus*, *Chrysosporium lobatum*, *Gibellulopsis nigrescens*, and order Pleosporales) and obligate alkaliphilic thermotolerant (*Sodiomyces magadii*, *S. tronii*, and sterile mycelium) ascomycetes. Thus the phenomenon of obligate alkaliphilia has been confirmed for ascomycetes, as well as their possible participation in the destruction of organic debris on the coast of the soda lake. An analysis of the taxonomic structure of the community of alkaliphilic and alkalitolerant fungi showed they belong mainly to the family Plectosphaerellaceae. Isolated fungi replenished the collection of extremophilic fungi, which are used as model objects to study the mechanisms of adaptation to various stress factors and as possible sources of valuable secondary metabolites.

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