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Review

Halotolerant and halophilic fungi

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ARTICLE INFO

Article history:

Received 24 June 2009

Accepted 2 September 2009

Available online 10 September 2009

Corresponding Editor:

Geoffrey Michael Gadd

Keywords:

Debaryomyces hansenii

Extremophiles

Hortaea werneckii

Molecular adaptations of halophilic fungi

Taxonomy of halophilic fungi

Wallemia ichthyophaga

ABSTRACT

Extreme environments have for long been considered to be populated almost exclusively by prokaryotic organisms and therefore monopolized by bacteriologists. Solar salterns are natural hypersaline environments characterized by extreme concentrations of NaCl, often high concentrations of other ions, high UV irradiation and in some cases extremes in pH. In 2000 fungi were first reported to be active inhabitants of solar salterns. Since then many new species and species previously known only as food contaminants have been discovered in hypersaline environments around the globe. The eukaryotic microorganism most studied for its salt tolerance is *Saccharomyces cerevisiae*. However, *S. cerevisiae* is rather salt sensitive and not able to adapt to hypersaline conditions. In contrast, some species like *Debaryomyces hansenii*, *Hortaea werneckii*, and *Wallemia ichthyophaga* have been isolated globally from natural hypersaline environments. We believe that all three are more suitable model organisms to study halotolerance in eukaryotes than *S. cerevisiae*. Furthermore, they belong to different and distant taxonomic groups and have developed different strategies to cope with the same problems of ion toxicity and loss of water.

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Introduction

Extreme environments have long been considered to be populated almost exclusively by prokaryotic organisms (Oren 2002), and therefore monopolized by bacteriologists. This also applies when the extreme conditions are caused by low water activity (a_w), as exemplified by studies of hypersaline environments. Here, the first studies on the presence of bacteria in such environments appeared in 1914 (Pierce 1914; Oren 2002), with no reports on the isolation of eukaryotic microorganisms from natural hypersaline habitats until more than 80 Y later (Gunde-Cimerman *et al.* 2000). Until then, fungi that could survive in low a_w were only known as

contaminants in food that had been preserved using high concentrations of salt or sugar.

In 2000, the first reports appeared showing that fungi are active inhabitants of solar salterns (Gunde-Cimerman *et al.* 2000). Since then, many new species, and indeed species only previously known as food contaminants, have been discovered in hypersaline environments around the World (Butin *et al.* 2005a; Zalar *et al.* 2005). These are now recognized as an integral part of indigenous microbial communities.

The aim of this review is to present the stable halophilic and halotolerant fungal communities that have been found in hypersaline waters of solar salterns. Additionally, we describe the most important adaptive mechanisms to life at

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doi:10.1016/j.mycres.2009.09.002

high salt, as shown by three model fungal organisms: *Debaryomyces hansenii*, *Hortaea werneckii* and *Wallemia ichthyophaga*.

Hypersaline environments

Crystalline salt (NaCl) is generally considered to be so hostile to most forms of life that it has been used for centuries as a food preservative. Food preserved with high concentrations of salt and the solar salterns that are found worldwide are instead domesticated and natural environments for halophilic and halotolerant microorganisms. These microorganisms can adapt to extreme concentrations of NaCl, and also often to high concentrations of other ions, to high ultraviolet (UV) irradiation and, in some cases, to extremes of pH (Gunde-Cimerman et al. 2000).

Multi-pond solar salterns that provide a full range of salinities have always been popular environments for studies on halophilic microorganisms. Of particular interest, there are the crystallization ponds, where NaCl saturation is reached. These ponds are coloured red by dense communities of *Halobacteriaceae*, β -carotene-rich *Dunaliella* cells, and by red species of Bacteria (*Salinibacter*). Recent studies have shown that pre-crystallization and crystallization ponds also harbour a surprisingly rich diversity and abundance of halophilic and halotolerant fungi (Gunde-Cimerman et al. 2000; Butinar et al. 2005a, b, c; Zalar et al. 2005, 2007, 2008), contrary to the general belief of a lack of mycobiota in such habitats (Javor 1989; Oren 1999; Pedrós-Alió et al. 2000). This new ecological finding is not only important for our understanding of microbial processes in natural hypersaline environments worldwide, but also for the not yet fully acknowledged contamination of food with fungi that are often mycotoxigenic, via the salt used as a preservative.

It is generally accepted in the solar salt industry that microorganisms and their products in the evaporating ponds can affect both the quality and quantity of salt that is eventually produced. Physical phenomena (evaporation, and deposition of calcium carbonate, gypsum and salt) are intimately linked to the biological systems, which can aid or harm the salt production (Javor 2002), and which can also “contaminate” the salt that is used for food preservation. Although it has long been recognized that haloarchaea can be introduced into food via solar salt, causing the spoilage of heavily salted proteinaceous products (Norton & Grant 1988; Grant 2004), the contamination of food with fungi via this salt has been overlooked.

Fungi in hypersaline environments

Until almost a decade ago, it was a general belief in mycology and in food microbiology that fungi growing on substrates with low a_w have a general xerophilic phenotype (Northolt et al. 1995) that is determined by the water potential of the medium, rather than by the chemical nature of the solute (Hocking 1993; Pitt & Hocking 1997). Therefore, fungi were considered xerophilic if they grow well at a_w of ≤ 0.85 , corresponding to 17 % NaCl or 50 % glucose added to their growth medium. In 2000, however, fungi were isolated for the first time from the brine of solar salterns (Gunde-Cimerman et al. 2000; Oren 2002). This and successive investigations revealed a consistent and stable species composition of mycobiota in

hypersaline environments worldwide, regardless of the geographic locality. This was seen as high fungal biodiversity of phylogenetically unrelated groups of fungi with minor local variations. The distribution of these fungal community structures and their abundance along environmental gradients showed that statistically the most important variables in their growth are two main nutrients (phosphorous and nitrogen), the dissolved oxygen, and the a_w , pH and year of sampling (Butinar et al. data not published).

These fungi that inhabit the natural hypersaline environments have a halophilic behaviour that is different from that of the majority of halophilic prokaryotes: with few exceptions, these halophilic fungi do not require salt for viability, as they can grow and adjust to the whole salinity range, from freshwater to almost saturated NaCl solutions (Plemenitaš et al. 2008).

Isolation and identification of halotolerant/halophilic fungi in hypersaline environments

These fungi were initially isolated from hypersaline water samples taken from seasonal solar salterns along the northern Adriatic coast, on the border between Slovenia and Croatia (Gunde-Cimerman et al. 2000). Later, hypersaline water samples were also taken from salterns that operated throughout the year in other geographic locations around the World, including the salterns along the Red Sea coast in Israel (Eilat), along the Mediterranean coast in Spain (Santa Pola and Ebro River Delta) and France (Camargue), along the Atlantic coast in Namibia (Skeleton coast), and along the coasts of the Dominican Republic (Monte Cristy), Puerto Rico (Fraternidad) and Portugal (Samouco). Hypersaline water samples have also been taken from the Dead Sea (Ein Bokek, Ein Gedi), the Great Salt Lake (Utah) and the Enriquillo Salt Lake (Dominican Republic) (Gunde-Cimerman et al. 2005).

Fungal population dynamics have been followed as described by Gunde-Cimerman et al. (2000). Different enumeration and selective media with increased concentrations of sugar and salt have been used for the isolation of the halotolerant/xerotolerant and halophilic/xerophilic mycobiota. After incubations of up to 14 weeks, the mean numbers of colony forming units (CFU) are calculated for these media.

The fungi that can grow *in vitro* at 3 M salt concentrations (a_w 0.85) and that are regularly isolated from global environments at salinities above 1.7 M have been characterized as halophilic (Gunde-Cimerman et al. 2005), whereas the sporadic isolates that can grow *in vitro* at 3 M NaCl are considered as halotolerant. Fungi have been mainly isolated from brine, and in some cases also from agar baits, biofilms on the surface of crystallization ponds, wood immersed in hypersaline waters, and more recently, microbial mats.

The main groups of halotolerant and halophilic fungi

Most halophilic and halotolerant fungi described to date from solar salterns have been identified either as known food-borne species with previously unrecognized natural niches, or as species that were not known to science, and consequently were newly described.

Although, at present there are a total of 106 orders of fungi known (Kirk et al. 2001), tolerance for low a_w is apparent in

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