Halophilic, Acidophilic, Alkaliphilic, Metallophilic, and Radioresistant Fungi: Habitats and Their Living Strategies

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Abstract

The magnificent stress-resistant mechanism, capacity to transform extreme abiotic factors as triggers for genetic modulation and physiological evolution, synced speciation in response to altered environment, and highly innovative succession cum resource management skill have crowned the microorganisms as the "specialist messenger of life" that thrive under extreme conditions. However, in recent decade, the ubiquitous fungi have gathered attention after archaea and bacteria for their versatile ecological adaptation, morphological resilience, and biochemical flexibility that allowed them to sustain and flourish under nature's deadliest environmental conditions. The inhospitable temperature, pressure, radiation, desiccation, salinity, and pH (both acidic and basic)-induced

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stress has capacitated a large number of extremophilic fungi with better sustainability factors. The "extraterrestrial" type of existence has been reported from hostile and lethal niches like frozen world of Antarctic and Arctic, deep sea ice and hydrothermal vents, hot springs, areas of high salt concentration, barren desert with extreme climate, toxic heavy metal and organic matter polluted regions, ocean trenches with high pressure, radiation contaminated zones, etc. The phylogenetic diversity of extremophilic fungi is highly complex exactly as their multidimensional mechanism of primary and secondary resource management, niche utilization, and physiological metabolism. From the bed of life-enriched rainforests to barren worlds full of toxic materials and fluctuating climate, this eukaryotic group has manifested great evolutionary plasticity and molecular strategies that are the center of interdisciplinary research that connects evolutionary biology, astrobiology, biochemistry, molecular biology, ecology, and many related fields of science. The modification of genetic make-up and introduction of specialized survival technique controlled via manipulation of metabolic pathways are not only associated with successful colonization of these fungal members but also important in terms of exploration of natural products from unexplored sources.

Keywords

Halophiles · Acidophiles · Alkaliphiles · Living strategy

9.1   Introduction

Until microbiologist exposed that the extreme environment of earth is truly occupied by a various range of microorganisms, humans assumed that in such extreme parameters no organism can live. Nonetheless, lately, a diverse variety of extremophiles has been discovered across a wide range of environment like hydrothermal vents, hot springs, polar regions, acid mine drainage sites, deserts, acidic lake, saline–alkaline lakes, sodic lakes, etc. (Gunde-Cimerman et al. 2003; Gunde-Cimerman and Zalar 2014; Plemenitaš et al. 2014; Selbmann et al. 2013). Extremophiles (eukaryotes, bacteria, and archaea) are microbes that have been found at extremes of pressures of up to 110 MPa, pH (0–12.5), temperature (122 °C − 20 °C), salinity (>1.0 M NaCl), and UV radiations. Archaea is the most flourish group of extremophiles. Alternatively, fungi are the most adaptable, ubiquitous, and effective ecological group having progressed gradually toward a wide range of ecological niches. Accordingly, they need to utilize prime sources for the establishment and production of essential enzymes. These fungi are additionally impacted upon by main abiotic factors like pH, salinity, temperature, and water availability and accessibility. Therefore, species of fungi occupy a respective niche due to their unique kind of survival mechanism based on particular ecological abiotic factors. Fungi apply diverse strategies to survive in different and extreme environmental conditions. These strategies are mainly C-selected (combative), S-selected (stress), and R-selected (ruderal) (Cooke and Whipps 1993). In this chapter, we are
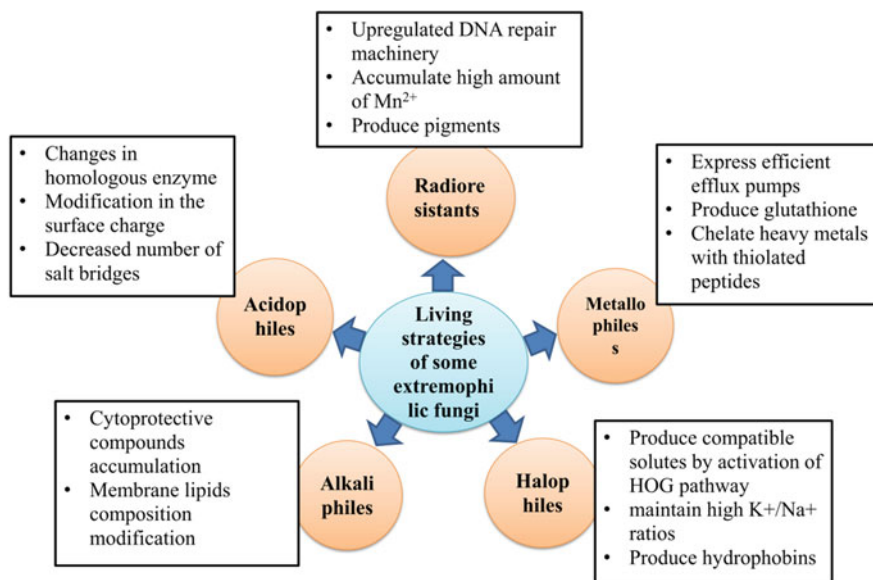
Fig. 9.1 Representative extremophilic fungi and their adaptive strategies to survive in extreme environmental conditions

specifically concerned with extremophilic fungi, which may use S-selected strategies for growth and survival in a range of so-called extreme environments. Extremophilic fungi are gaining ecological importance as well as biotechnical interest due to their ability to produce different kinds of bioactive compounds, enzymes, and proteins with prospective application in the industrial fields. Extremophilic fungi have some unique feature that were evolved based on extreme environmental conditions. Types of extremophilic fungi and its adaptative strategies to survive in extreme environment conditions are presented in Fig. 9.1. Many of the biomolecules, viz., enzymes and proteins produced by these fungi, are attributed to some defense strategies for their survival in the extreme environment. Apart from industrial benefits, these fungi possess unique genes that promote the growth of plant when applied as biofertilizers in sustainable agriculture (Yadav 2017). Thus, this chapter focuses on the strategies adopted by the other extremophilic fungi (halophiles, acidophiles, and alkaliophiles) to grow in harsh environments linked to some genes' expressions and the production of natural products as a response, which lead to an ecological impact on the environment.

9.2 Halophiles

Halophilic fungi require more than 0.2 M salt for their growth and are divided into (1) slight halophiles (0.2–0.85 M; 2–5%), (2) moderate halophiles (0.85–3.4 M; 5–20%), and (3) extreme halophiles (3.4–5.1 M; 20–30%) (El Hidri et al. 2013; Guesmi et al. 2013).

9.2.1   Habitats

Halophilic fungi have been reported from various habitats including the following.

9.2.1.1 Saline Soil
A saline soil is soil with high but variable sodium concentration.

9.2.1.2 Saline Water
Saline water is water with salinity 3% or above (De-Dekker 1983). It includes brackish water, marine water, and water from salt lakes and salterns. The saline water is broadly divided into two types, viz., NaCl-rich thalassohaline and $MgCl_2$- and $CaCl_2$-rich athalassohaline. Of these, thalassohaline water is an important habitat of halophilic life including fungi. Some typical thalassohaline habitats are the Dead Sea, Grate Salt Lake of USA, and Natrun Valley of Egypt. The Dead Sea is about 320 m in depth and a salt concentration of 78% NaCl. It has slightly acidic pH and important ions such as Na+, Cl-, and Mg2+ (Javor 1989). The Great Salt Lake, USA, has slightly alkaline pH and salinity of 33% NaCl (Javor 1989). The Solar Lake, Egypt, may have salinity of 20% NaCl in the summer. Lakes at Natrun Valley (Wadi El Natrun), Egypt, have salinity in the range of 3.1–8.6% NaCl,

9.2.1.3 Solar Salterns
These are manmade series shallow ponds for making salt. The ponds are fed by sea water or other saline water bodies, the last in the series is crystallizer having salt above 30% (Antón et al. 2000). Inland saltern of La Mala, Spain, has salinity of 18% NaCl and other ions like Mg2+, Ca2+, and K+.

9.2.2   Halophilic and Halotolerant Fungi

The fungi isolated from various saline habitats are mostly halotolerant rather than halophilic. They can grow in growth medium supplemented with or without salt. They have been isolated from saline and nonsaline habitats (Plemenitaš et al. 2008) including from food as food contaminants. The orders Capnodiales, Eurotiales, and Dothideales of Ascomycota and the genus Wallemia of Basidiomycota have been reported to comprise halophilic or halotolerant species (Al-Abri 2011). They include meristematic melanized yeast-like fungi, the so-called black yeasts such as *Hortaea werneckii* (Zalar et al. 1999b), *Phaeotheca triangularis* (Zalar et al. 1999b, c), *Aureobasidium pullulans* (Zalar et al. 1999b), and a new species *Trimmatostroma salinum* (Zalar et al. 1999a), different related species of the genus *Cladosporium* (Gunde-Cimerman et al. 2000; Zalar et al. 2007; Butinar et al. 2005a), non-melanized yeasts *Pichia guilliermondii*, *Debaryomyces hansenii*, *Yarrowia lipolytica*, *Candida parapsilosis*, *Rhodosporidium sphaerocarpum*, *R. babjevae*, *Rhodotorula laryngis*, *Trichosporon mucoides*, *Metschnikowia bicuspidata*, *Candida atmosphaerica*-like and *Pichia philogaea*-like (Butinar et al. 2005b), the filamentous genera *Wallemia*, *Scopulariopsis* and *Alternaria* (Zalar et al. 2005;

Gunde-Cimerman et al. 2005), and different species of the anamorphic genera *Aspergillus* and *Penicillium*, including some of their teleomorphic genera *Eurotium* and *Emericella* (Butinar et al. 2005, 2011). Of all, *Wallemia ichthyophaga* (Basidiomycetes) is the most well-known and in true sense halophilic fungus that requires a minimum of 10% NaCl for its growth (Zalar et al. 2005; Zajc et al. 2014).

9.2.3   Living Strategies

9.2.3.1 Lower Water Activity

Halotolerants are adapted to lower water activity (a_w) and can thrive in the presence of lower concentration of available water.

9.2.3.2 Compatible Solute

Fungi face in hypersaline environment two stresses, viz., osmotic and ionic ones. Fungi adapted to life at a_w do this by accumulating compatible solutes to counter the impact of lowering turgor pressure in the presence of hypersaline environment. They apply same strategy to counter salinity-related osmotic stress. The halophilic *W. ichthyophaga* and halotolerants *A. pullulans*, *H. werneckii,* and other halotolerant fungi accumulate primarily glycerol as compatible solute. In addition, *W. ichthyophaga* does accumulate little amount of arabitol and traces of mannitol to supplement glycerol (Zajc et al. 2013a, b). The black yeast *H. werneckii,* on the other hand, at lower salinities produces mycosporine–glutaminol–glucoside (prime function of mycosporine being involved in fungal sporulation and UV protection) (Oren and Gunde-Cimerman 2007), and at higher salinities produces other polyols (e.g., erythritol, arabitol, and mannitol) to supplement glycerol (Kogej et al. 2004, 2006). In case of salt-tolerant yeasts *Debaryomyces hansenii*, *Candida versatilis*, *Rhodotorula mucilaginosa*, or *Pichia guilliermondii* trehalose and other polyols supplement glycerol (Andre et al. 1988; Prista et al. 1997; Almagro et al. 2000).

9.2.3.3 Ion Homeostasis

There are at least three physiological strategies halotolerant fungi apply to overcome ion stress. The halotolerant *H. werneckii* is said to use the two salt-responsive P-type (ENA-like) ATPases (Gorjan and Plemenitas 2006) to extrude Na + at higher concentration of NaCl as supported by genomic data (Lenassi et al. 2013). The halophilic *Wallemia ichthyophaga,* which lacks most cation transporters, seems to use avoidance strategy by preventing entry of excess Na + with its extremely thickened cell walls (Kralj Kuncic et al. 2010, 2013; Zajc et al. 2013a, b).
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9.2.3.4 Cell Wall Structure and Pigmentation

At the differential level of melanin on outer cell wall of *H. werneckii* in the presence of different salt concentrations (e.g., thin layer of melanin when there is no NaCl, but thick layer of melanin at optimal salt concentration) (Kogej et al. 2004, 2006), the melanin seemingly gives mechanical support to counter higher turgor pressure

(Kogej et al. 2004, 2006). The meristematic growth of *Wallemia ichthyophaga* forming bigger (fourfold) and compact multicellular clumps and thickened (three-fold) at higher salinity (cf. growth phenotype at lower salt concentration) is considered as an important adaptation to tolerate extreme salinity (Kralj Kuncic et al. 2010, 2013).

9.2.3.5 Plasma Membrane Fluidity

It is generally seen that eukaryotic cells that accumulate glycerol as a compatible solute, its back outflow has to be stopped by using active transport system (energetically costly) or by reducing fluidity of membrane through enhancing sterol content (Oren 1999). In case of *H. werneckii*, it has been shown that membrane remains fluid over a wide range of salinities (Turk et al. 2004, 2007) and its sterol content remains largely unchanged (Turk et al. 2004), suggesting that its hypermelanized cell wall also helps maintain glycerol at higher concentrations in the cells even in the presence of highly fluid membrane (Gostincar et al. 2009).

9.2.3.6 Molecular Basis

Halophilic and halotolerant fungi developed a novel molecular mechanism so that they can maintain their growth in high salt condition. Halophilic fungi possess a few features for osmotolerance via utilizing compatible solutes by activation of the HOG pathway. The HOG pathway produces glycerol that reestablishes the osmotic balance in the cell (Gostinčar et al. 2011; Zajc et al. 2012; Hohmann 2009). Plemenitaš et al. (2014) observed that halophilic *W. ichthyophaga* produced compatible solutes (glycerol) by HOG pathway activation implicated to their survival in a high osmolar environment. *W. ichthyophaga* also maintains high K^+/Na^+ ratios since in a high saline environment toxic Na^+ ions are over K^+ ions. Thus, halophilic fungi developed some mechanisms that can maintain high K^+/Na^+ ratios (Plemenitaš et al. 2014). Hydrophobin is a type of protein that contains a high number of acidic amino acids. These acidic amino acids are exposed to the protein surface and bind with salt and reduced salt-induced changes (Siglioccolo et al. 2011). Hydrophobins were found to be present in both *W. ichthyophaga* and *W. sebi* (Zajc et al. 2013a, b). Hydrophobins also induced microconidial chain formation in *W. ichthyophaga*, which might involve the accumulation of cells for the formation of the cluster. Production of haloadaptation is primarily attributed to the response against salt stress (Fuchs et al. 2004; Gostincar et al. 2010). Hydrophobins can also maintain cell wall rigidity so that halophilic fungi take advantage of osmolarity changes in stress (Wosten 2001; Bayry et al. 2012). *H. werneckii* contains acidic proteins that are involved in the accumulation of K^+ ions besides glycerol in response to hypersalinity (Kogej et al. 2005).

9.3   Alkaliphiles

Biochemical processes can occur at different hydrogen ion concentrations. However, biochemical events function better close to neutral pH. Very high or low pH harms the activity of biochemical events mostly via damaging the protein structure. Alkaliphiles have been defined as organisms that grow optimally at pH above 9. Alkaliphiles are further divided into obligate alkaliphiles (incapable of growing at or below pH 7.0) and facultative alkaliphiles (capable of growing at pH 7.0) (Padan et al. 2005; Slonczewski et al. 2009).

9.3.1   Habitats

Alkaline habitats have been classified into

1. High Ca^{2+} environments (groundwaters bearing high CaOH). Various locations of this type have been reported in California, Oman, the former Yugoslavia, Cyprus, Jordan, and Turkey (Barnes et al. 1982; Jones et al. 1994).
2. Low Ca^{2+} environments (e.g., soda lakes, soda soil, and deserts with major salt being sodium carbonate) (Grant and Horikoshi 1989, 1992). These are stable environments with soda lakes being a productive system because of the presence of favorable temperatures (30–45 °C), high sunlight intensities, and abundance of HCO3 for photosynthesis (Ulukanli and Diurak 2002). The soda lakes are characterized by higher pH (11–12) and around of 5–30% salinity ($NaCO_3$ and NaCl in almost equal proportion) conditions (Duckworth et al. 1996).

   Alkaliphiles are also found in a few insect guts and littoral soils (Hicks et al. 2010).

9.3.2   Alkaliphilic Fungi

Alkaliphilic fungi are very rare and reported sporadically from soda soil, soda lake, and limestone cave (Nagai et al. 1995, 1998; Grum-Grzhimaylo et al. 2013a). Alkalitolerant fungi *Fusarium oxysporum*, *F. bullatum,* and *Penicillium variabile* capable of growing at pH have been isolated in 1923 (Johnson 1923). Okada et al. (1993) isolated alkaliphilic fungus *Acremonium alcalophilum* growing optimally at pH 9.0. Most of the fungi thus isolated were alkalitolerants that can grow at alkaline pH of 10. For example, *Acremonium alternatum*, *A. furcatum*, *Acremonium* sp. 6, *Gliocladium cibotii* (YBLF 575), *Phialophora geniculata*, *Stachylidium icolor,* and *Stilbella annulata* isolated from soil *Acremonium* sp. 6 were said to be alkalophile (Nagai et al. 1995). Likewise out of six *Acremonium* and *Chrysosporium* species from limestone caves (stalactite caves) in Japan capable of growing at alkaline pH, one species each of *Acremonium* sp. and *Chrysosporium* sp. were alkalophiles (Nagai et al. 1998). Then eight species of alkaliphilic and alkalitolerant

soil fungi from Argentina have been reported belonging to families *Bionectriaceae*, *Trichocomaceae*, *Sporormiaceae*, *Ceratostomataceae,* and *Sordariaceae* (Elíades et al. 2006). Generally, the alkaliphilic fungi are anamorphic without forming any sexual structure, for example, *Acremonium* or *Verticillium* species (Okada et al. 1993; Kladwang et al. 2003). An alkaliphilic fungus *Sodiomyces* alkalinus showing optimal growth at alkaline pH, however, is able to form cleistothecium (Grum-Grzhimaylo et al. 2013b). Another novel alkaliphilic fungus *Emericellopsis alkalina* sp. nov. (grow at pH 4–11.2, but optimally at 10–10.2) besides several alkalitolerant isolates of *Acremonium* has been reported (Grum-Grzhimaylo et al. 2013b).

9.3.3   Living Strategy

The fungi found in soda soil/water face at least three stresses, namely, high osmotic pressures, low water potentials, and elevated ambient pH (>9) (Grum-Grzhimaylo et al. 2013b).

   Alkylophilic fungi regulate their internal pH near neutral through active and passive regulation mechanisms. Passive regulation involves the low membrane permeability and cytoplasmic pools of polyamines (PA). Active regulation mechanism of homeostasis involves the sodium ion channels (Sharma et al. 2017). Cell wall components are very different in alkaliphiles. Many acidic polymers are present on the cell wall that reduces the pH. Altered membrane lipids and presence of cytoprotectant molecules enable them to survive at alkaline pH (Masato et al. 2010). Na^+/H^+ and K^+/H^+ type of antiporters are used to produce acid to reduce the internal pH and thus regulate the proton motive force (Charlesworth and Burns 2016). They employ different adaptation mechanisms against stress via accumulation of cytoprotective compounds (carbohydrate osmolytes) and modification of the composition of their membrane lipids. *Sodiomyces alkalinus* (Plectosphaerellaceae, Sordariomycetes, Ascomycota) is an alkalophilic fungus that accumulates cytosol carbohydrate trehalose, mannitol, phosphatidylcholines (PC), and PA in the mycelium of the fungus. Fruit bodies of this fungus were detected with high amounts of trehalose, triacylglycerols (TAG), PC, and sterols (Kozlova et al. 2019a). Bondarenko et al. (2018) observed trehalose, mannitol, and arabitol accumulation in two obligate alkaliphilic fungi *Sodiomyces magadii* (Plectosphaerellaceae, Sordariomycetes, Ascomycota) and *S. alkaline* (Plectosphaerellaceae, Sordariomycetes, Ascomycota) with almost double proportion of PA and lower proportions of PC and St (Bondarenko et al. 2018). Kozlova et al. (2019b) demonstrated unique features of Ascomycete *S. alkalinus*, which in the early lysis of cell walls of asci releases immature ascospores inside the fruit body whereas pseudoparenchymal and peridium cells degradation occur long before the ascospores maturation at extremely high pH of soda lakes. After maturity, these ascospores are forcefully released due to higher turgor pressure by cracking the fruit body. It was assumed that these features could develop to cope with the high pH (Kozlova et al. 2019b).

The fungi *Fusarium oxysporum,* was found to respond to hypersaline conditions by the expression of gene *ena1* encoding P-type Na^+A-ATPase. This gene is also upregulated when the pH of growth environment is increased (Caracuel et al. 2003). This coincidence suggests commonality of alkalitolerance and halotolerance mechanisms.

9.4   Acidophiles

Acidophiles are organisms that grow optimally at pH < 4.0. Another criterion to differentiate acidotolerant and acidophilious is the growth curve; the former exhibits bimodal growth while the latter shows unimodal growth (Cavicchioli and Torsten 2000; Gimmler et al. 2001). Fungi are mostly found to be acidotolerants.

9.4.1   Habitats

The acidophilic fungi may be isolated from neutral or acidic habitats (pH < 3) such as acidic soil, lake, swamp, and peat bogs (Middelhoven et al. 1992). Some of the highly studied sites are solfatara soil studied in the USA, Japan, Russia, Italy, Iceland, New Zealand, acid rock drainage of São Domingos (Portugal) and Rio Tinto (Spain), etc.

9.4.2   Acidophilic Fungi

Acidophilic fungi are rarely found; generally fungi growing at lower pH can also grow at neutral to slightly alkaline pH and thus mostly they are acidotolerant. Fungal biodiversity study in highly acidic Tinto river (Spain) revealed species of *Scytalidium*, *Bahusakala*, *Phoma*, *Heteroonium*, *Lecythophora*, *Acremonium,* and *Mortierella* (López-Archilla et al. 2004).

Three highly acidotolerant fungi *Acidothrix acidophila* (Amplistromataceae, Sordariomycetes, Ascomycota), *Acidea extrema,* and *Soosiella minima* (Helotiales, Leotiomycetes, Ascomycota) have been isolated from highly acidic soils in the Czech Republic and a coastal site in the Antarctic Peninsula (Hujslová et al. 2014) while another anamorphic brown mold fungus *Scytalidium acidophilum* was isolated from acidic soil and acidic solutions in an industrial plant and a uranium mine that show optimum growth at acidic pH (Sigler and Camichaeil 1974).

Acidophilous fungi have been explored from Iberian Pyrite Belt (IPB), and acid rock drainage in two localities São Domingos (Portugal) and Rio Tinto (Spain). The most acid-tolerant found was yeast Cryptococcus spp. 5 followed by *Cryptococcus* spp. 3 and Lecytophora spp. Moderately tolerant species were *Candida fluviatilis*, *Rhodosporidium toruloides*, *Williopsis californica*, and three unidentified yeasts belonging to *Rhodotorula* and *Cryptococcus* (Gadanho et al. 2006).

A novel acidophilic fungus *Teratosphaeria* (Capnodiales, Dothideomycetes) was reported from biofilms collected from an extremely acidic and hot spring. It is a ascomycetous teleomorphic fungus belonging to ascomyetes; phylogenetically close to *Acidomyces acidophilus* and *Bispora* spp., earlier reported acidophilic anamorphic fungi (Yamazaki et al. 2010).

From various studies, the domination of dematiaceous fungal species has been found in various acidic habitats (Amaral Zettler et al. 2002, 2003; Baker et al. 2004, 2009; Hujslová et al. 2010, 2013; López-Archilla et al. 2004). Of these, the three fungi *Acidomyces acidophilus* (Selbmann et al. 2008), *Hortaea acidophila* (Hölker et al. 2004), and *Acidomyces acidothermus* (Yamazaki et al. 2010; Hujslová et al. 2013) have been considered as acidophilic ones. All these plus the acidotolerant fungus *Acidiella bohemica* (Hujslová et al. 2013) belong to the family Teratosphaeriaceae (Capnodiales, Dothideomycetes, Ascomycota). Moreover, the three fungal species *A. acidophilus*, *A. acidothermus,* and *H. acidophila* along with two unidentified fungal isolates *Paecilomyces* spp. and *Penicillium* sp. 4 can grow at pH 1 (Gimmler et al. 2001; Hölker et al. 2004; Hujslová et al. 2010; Yamazaki et al. 2010).

9.4.3 Living Strategy

Fungi being eukaryotes face four main challenges: very high H^+ concentration, higher concentration of toxic metals, oligotrophic conditions, and extreme temperatures (Whitton 1970; Brock 1978; Brake and Hasiotis 2010). Extremely low pH irreversibly destroys primary and secondary structures of proteins (Kapfer 1998; Nixdorf and Kapfer 1998).

The acidotolerants employ twin mechanisms to tolerate hyperacidic environments; extrusion of protons out of the cell and maintaining low proton membrane permeability (Nikolay et al. 2018). Fungi by virtue of these internal pH regulation mechanisms exist commonly in acidic environments (Gross and Robbins 2000).

Acidophiles maintain the intracellular pH by preventing proton influx, buffering of intracellular protons, and efflux of protons. Although a number of protein transporter systems are located on the cell membrane to regulate the cytosolic pH levels (Gupta et al. 2014; Sharma et al. 2017; Christel 2018).

Acidophiles have highly impermeable cell membrane or reduced size of membrane pore to reduce entry of protons into the cytoplasm and maintain the pH homeostasis (Mirete et al. 2017) or have efficient proton pumps, which maintain the proton gradient across the cytoplasm and its pH at or near neutral pH (Mirete et al. 2017). They cope with the heavy metals by rapid efflux of these metals, inactivate them, or convert them into less toxic compounds (Charlesworth and Burns 2016; Christel 2018) and manage their oxidative stress by regulating the reacting oxygen species (ROS). They possess some antioxidants such as glutathione to inactivate these ROS or possess some enzymatic machinery such as superoxidase mutase or peroxidase to neutralize or inactivate the ROS (Christel 2018). They have

highly expressed chaperons that help them in rapid repair of the damaged proteins. The protein protects the DNA and other proteins from damage caused by the low pH (Mirete et al. 2017). An acid-tolerant strain of *Penicillium funiculosum* growing actively at pH 1.0 possesses a major facilitator superfamily transporter (PfMFS) involved in the acid resistance and intracellular pH homeostasis (Xu et al. 2014).

Acidophilic microorganisms are ecologically and economically important extremophiles found in solfataric fields, hydrogen sulfide (H_2S) emissions, active or abandoned mines, acidic copper mine wastes, and geysers (Sharma et al. 2012). Although a few acidophiles have been studied up to now, those data are not yet sufficient to clearly understand the adaptive features of acidophilic fungi. Determination of endo-1,4-b-xylanase crystal structure from *Scytalidium acidophilum* (Chaetomiaceae, Leotiomycetes, Ascomycota), XYL1 acidophilic fungi adds understandings of low pH adaptation. This study revealed the changes in the homologous enzyme to maintain stability in an acidic environment. Alterations include modification in the surface charge, decreased number of salt bridges, changes like the conserved residue of the active site, etc., at low pH (Michaux et al. 2010). Bacteria control internal low pH through increasing ATPase pump efficiency, which rapidly pumps out protons from the cells to raise the internal pH of the cell. Bacterial adaptation in such an environment (low pH) includes alternation of the cell membrane and controlling of flagella. This kind of observation is lacking in fungi and needs to be elaborated to enable a better understanding of fungi present in such ecological niches.

9.5   Metallophiles

Metallophiles are the organisms that thrive under metal-rich condition or environment with high metallic concentration. They are able to tolerate and detoxify high concentration of heavy metals. Most of the metallophiles are acidophiles, thus enhancing their survival 1000-fold than mesophiles and efficiently tolerate the high level of heavy metals (Anahid et al. 2011; Gupta et al. 2014).

9.5.1   Habitat

Naturally metal-rich environment such as water bodies and land around mining areas are the main habitats of metallophiles. Apart from these metal-contaminated areas around industries are also habitats of such metallophiles.

9.5.2   Metallophilic Fungi

Penicillium verrucosum KNU3 is metallophilic as it shows increased growth in the presence of Cr^{3+}, Cu^{2+}, and Pb^{2+} at 1 mM concentration (Joo and Hussein 2012). Similarly, *Penicillium simplicissimum* shows higher growth in the presence of heavy

metals at concentration up to 8000 ppm (Anahid et al. 2011). Other fungi *Aspergillus niger*, *Aspergillus foetidus* and *P. simplicissimum* showing high tolerance to molybdenum and vanadium have been reported. Of these, *P. simplicissimum* and *A. foetidus* are adapted to high concentration of heavy metals and show enhanced growth in the presence of heavy metals up to concentration of 2000 ppm (Valix et al. 2001).

Fungi that are tolerant to various metals have also been reported. For example, chromium- and nickel-resistant *Aspergillus* sp. tolerating chromium toxicity up to 10,000 mg/L chromium have been reported (Congeevaram et al. 2007). Ectomycorrhizal fungi *Hymenogaster* sp., *Scleroderma* sp., and *Pisolithus tinctorius* show higher tolerance against increased concentration of Al, Fe, Cu, and Zn (Tam 1995). Heavy metal biosorption analysis revealed that *Aspergillus* sp.1 accumulated 1.20 mg Cr and 2.72 mg Cd, *Aspergillus* sp. 2 accumulated 1.56 mg Cr and 2.91 mg Cd while *Rhizopus* sp. accumulated 4.33 mg Cr and 2.72 mg Cd per gram of biomass (Zafar et al. 2007). *Saccharomyces cerevisiae* and *Rhizopus nigricans* accumulate zinc (Sprocati et al. 2006). *Fusarium solani* shows tolerance to Ag (I) up to 1100 mg/L concentration (El Sayed and El-Sayed 2020). Another strain of fungus *A. niger* tolerates high concentration of heavy metal (Acosta-Rodríguez et al. 2018). *Fomitopsis meliae*, *Trichoderma ghanense*, and *Rhizopus microsporus* are some other metalloresistant filamentous fungi isolated from gold and gemstone mine sites that can tolerate various heavy metals such as Cu, Pb, and Fe (Oladipo et al. 2018).

9.5.3   Living Strategies

Presence of heavy metals such as Zn, Cd, Hg, Pb, Ag, Co, and Cr makes the environment very toxic. Generally high metal concentration inhibits the growth and functioning of microbes, but metallophiles develop the strategies to function optimally under these conditions. Some metallophiles possess efficient efflux pumps for the rapid removal of toxic metals while others associate these metals by binding them with protein molecules (Gupta et al. 2014). Ascomycete fungi such as *S. cerevisiae*, *Schizosaccharomyces pombe,* and *Candida albicans* have been studied for their adaptations to cope with high concentration of heavy metals. Some fungi chelate these heavy metals with thiolated peptides and make a complex that is either accumulated in the vacuole or extruded out of the cell. Some produce an antioxidant glutathione in high amount that prevents the oxidative stress. *S. cerevisiae* transports the heavy metals into external environment through a plasma membrane transporter Pca1 (Otohinoyi and Omodele 2015). They exhibit two general mechanisms: extracellular and intracellular, to fight with the high concentration of heavy metals. Extracellular mechanism involves the chelating and cell wall binding (biosorption) of heavy metals to restrict the entry of heavy metals into the cell while intracellular mechanism involves the binding of heavy metals to proteins to reduce the concentration of heavy metals inside the cell and prevent itself from damage (Anahid et al. 2011).

9.6 Radioresistants

Radioresistants or radiophiles are the extremophiles that are highly resistant to high level of ionizing and ultraviolet radiation. Radioresistant organisms tolerate extreme radiations for longer period of time while radiotolerant organisms tolerate extreme radiations for only a short period of time. Ionizing radiation such as gamma radiation and nonionizing radiation such as ultraviolet radiation are the two major radiations that cause lethal effect on an organism. Radiophiles are polyextremophiles as they can tolerate extreme cold, dehydration, vacuum, and high acidic concentration (Coker 2019).

9.6.1 Adaptations of Radiophiles

Gamma radiations causes double-stranded breaks in the DNA of an organism and produce reacting oxygen species that interfere with the metabolic processes leading to cell death. They also damage proteins and lipids and produce persistent oxidative stress. UV radiations cause more destruction by DNA damage through formation of thymine dimer and pyrimidine radio tolerant photoproducts. Radiophiles protect them from gamma radiation by adapting efficient DNA repair mechanism that rapidly repairs the damaged DNA, production of antioxidants, enzymatic defense system (increased production of enzyme such as catalase to inactivate free radicals and reactive oxygen species), and condensed nucleoid. UV-resistant radiophiles protect them from radiation through multiple mechanisms. Their genome is composed of very small number of bipyrimidine sequences. They possess gene duplication phenomenon causing polyploidy. Carotenoids, superoxide dismutase, and hydroperoxidases reduce the stress developed by radiation (Coker 2019). Radiophiles possess the capability to survive under starvation and high oxidative stress condition. They can even survive in condition with high amount of DNA damage. Ionizing radiations induce changes in upregulation of cell repair system and genetic component of an organism. Some UV radiation-resistant radiophiles protect their DNA from lethal radiation by the presence of UV-absorbing pigments such as scytonemin in sheath around the cell while some radiophiles accumulate UV-absorbing pigments such as mycosporine like amino acids in the cytoplasm of the cell (Dighton et al. 2008; Kazak et al. 2010).

Fungi are resistant to chronic ionizing radiations evolved from various radiation sources such as radioactive waste and nuclear disaster. The main strategy adopted by the radiation-resistant fungi against high radiation stress is to scavenge reactive oxygen species. They accumulate high amount of Mn^{2+} metabolite antioxidant complex for scavenging reactive oxygen species induced by the ionizing radiations as Mn^{2+} complexes with other compounds to inactivate the reactive oxygen species. Low concentration of iron ions and high concentration of manganese ions protect the cell from oxidative stress. Radiotolerant fungi possess high Mn^{2+}/Fe^{2+} ratio (Dadachova and Casadevall 2008; Dighton et al. 2008; Matusiak 2016). Melanin and some other pigments play an important role for the development of resistance to

radiations. A complex polymer melanin is important in energy transduction and shielding as they possess the capability to absorb various kinds of electromagnetic radiations. Radiation exposure causes fungal melanin pigment to alter the shape and induce them to form a thick layer of melanin. Some fungi, especially melanized fungi, harvest energy from the radiation with the help of melanin pigment and utilize this energy for their growth and development (Dadachova and Casadevall 2008; Dighton et al. 2008).

Ascomycota yeast possess resistance to chronic ionizing radiation is correlated with Cr^{+3} while resistance of Basidiomycete yeast to chronic ionizing radiation is correlated with the highest temperature that allows the growth (Shuryak et al. 2019). Biofilms of radioresistant fungi are adapted to high mutation rate and are more resistant to ionizing radiation than other radioresistants (Ragon et al. 2011). *Cryptococcus neoformans* is a radioresistant fungi that generally can be found in high radiation environment. Genome-wide radiation resistance analysis of this fungus explains the upregulation of DNA repair machinery for reducing the radiation stress. Rad53 protein kinase regulates the transcription factor Bdr1 and controls the transcription (Jung et al. 2016).

9.7   Fungi in Exoplanet-like Environment

For the study of life outside of our planet, extremophilic organisms are considered the best suitable model. As we already discussed, these organisms can survive in extreme acidic, alkaline, heat, cold, salt, and pressure. The real challenges to grow extremophilic fungi in exoplanet-like environment are space vacuum, solar, galactic and ionizing radiation, and extreme cold and heat. The precondition for Mars would be water availability. Fungi-producing melanin pigment are mostly colonized in the Antarctic to the Arctic to high-altitude terrains. For growing in such regions, extremophilic fungi have to deal with UV radiations, dry, and cold. So, melanized fungi could be a suitable model for studies in Mars-like habitat. Microcolonial fungus *Cryomyces antarcticus* (incertaesedis), Dothideomycetes, Ascomycota) can live in Mars-like habitat in a good way. *C. antarcticus* in Mars-like habitat for 24 h showed a decrease in protein number, but after 4- and 7-day treatment protein number was increased again and protein patterns matched to normalcy. This result indicated that *C. antarcticus* needs 1 week for recovery of its metabolic activity in a Mars-like condition (Zakharova et al. 2014). Another melanin-forming fungi *Cryomyces minteri* (incertaesedis, Dothideomycetes, Ascomycota) and known *C. antarcticus* exposed in Mars-like habitat for 18 months resulted in 10% of the sample being able to form colonies. Additionally, high stability in DNA is also observed in the hostile conditions of space (Onofri et al. 2015). Onofri et al. (2018) isolated *C. antarcticus* and *C. minteri* from cryptoendolithic microbial communities in Antarctica. After the screening of their DNA, it was observed that *C. antarcticus* displayed higher resistance than *C. minteri*. They concluded that the apparent presence of thicker melanized cell wall of *C. antarcticus* could be a reason for higher resistance (Onofri et al. 2018). Pacelli et al. (2019) experimented with black

fungus *C. antarcticus* with a simulated space vacuum or Mars-like condition and found that this black fungus can tolerate such a condition with high integrity of DNA even after the treatments (Pacelli et al. 2019) So the theory that in space biological material can be preserved is somehow true as we cited that fungi DNA remains undamaged in space. However, exact space condition cannot be created in the laboratory.

9.7.1 Genes and/or Secondary Metabolites

The EhHOG gene has an important role in the osmoregulatory pathway. EhHOG gene, isolated from *Eurotium herbariorum* from the dead sea, where salinity is the utmost on earth, showed resistance against salt, water, and low- and high-temperature stress. EhHOG genes encode mitogen-activated protein kinase (MAPK), which is a homolog of the HOG gene from *Aspergillus nidulans, Saccharomyces cerevisiae, Schizosaccharomyces pombe,* and many other eukaryotes. In the hog1 mutant gene of *S. cerevisiae*, when supplemented by the EhHOG gene, growth of the fungi is restored in high salt stress condition. Additionally, glycerol content also increased (Jin et al. 2005). Halophilic fungus *Aspergillus glaucus* contains RPL44 (ribosomal protein L44), a conserved protein related to salt resistance (Liu et al. 2014). Same kind of result was found in aquaglyceroporins (GlpFs), 60S protease subunit, and AgRPS3aE, ribosomal subunit from *A. glaucus*. Aquaglyceroporins transport glycerol and water, which are related to osmoregulation (Liang et al. 2015; Liu et al. 2015). Altogether these genes are highly conserved; they can support transgenic plants or cells surviving under high salt and heat stress conditions. Analysis of these genes may further support genetic engineering tools and crop improvement under high salt, water, and temperature stress. Extremophilic fungi develop exclusive defenses to survive in extreme conditions like temperature, salinity, pH, pressure, and desiccation, which leads to the production of diverse secondary metabolites. Secondary metabolites have no direct role in the adaptation process of extremophilic fungi. However, they have an indirect role by inhibiting the different microorganisms (viruses, pathogenic fungi, and pathogenic bacteria) in a competition to survive in an environment with limited nutrients (Table 9.1).

9.8 Conclusion

Extremophilic features are great parts of evolution, and scientists would get a better understanding of the effect of different proteins, genes, or metabolites responsible for survival in extreme environments. The presence of several harsh environmental conditions can lead to weighty challenges for living, resulting in unique survival strategies. Fungi are one of the most adaptable organisms for their splendid environmental and structural flexibility. They are physiologically changed for vigorous growth under extreme temperature, salt, pressure, pH, and minimal water availability through employing biochemical pathways, which are responsible for synthesizing

Table 9.1 List of antimicrobial activity of metabolites from extremophilic fungi

Category	Species	Collected from	Compound	Antimicrobial activity against	Reference
Acidophiles	*Penicilliumpurpurogenum* JS03–21	Red soil	Purpurides B, purpurides C berkedrimane B	*Candida albicans, Enterobacter aerogenes, Pseudomonas aeruginosa*	Wang et al. (2013)
Halophiles	*Aspergillus flavus, aspergillus gracilis, aspergillus penicillioides*	Solar saltern	Not mentioned	Not mentioned	Ali et al. (2014)
Psychrophiles	*Penicillium chrysogenum*	Benthisenviornment	Rugulosin, skyrin	*Staphylococcus aureus, Escherichia coli, Candida albicans*	Brunati et al. (2009)
Piezophiles	*Aspergillus* sp. SCSIO Ind09F01	Deep sea	Liotoxin, 12,13-dihydroxy-fumitremorgin C, helvolic acid	*Mycobacterium tuberculosis*	Luo et al. (2017)
	Aspergillus versicolor	Deep sea	Anthraquinone	Methicillin-resistant *Staphylococcus aureus*	Wang et al. (2018)
	Neosartorya fennelliae KUFA 0811	Marine sponges	Dihydrochromone dimer	*Staphylococcus aureus ATCC 29213, Enterococcus faecalis ATCC 29212*	Kumla et al. (2017)
	Oidiodendron griseum UBOCC-A-114129	Deep sea sediment	Dihydrosecofuscin/ secofuscin	*Enterococcus faecalis*	Navarri et al. (2017)
Thermophiles	*Elaphocordyceps ophioglossoides*	Soil	Ophiosetin	Not mentioned	Putri et al. (2010)
Xerophilies	*Aspergillus felis*	Atacama Desert	Cytochalasins	*Paracoccidioides brasiliensis Pb18*	Mendes et al. (2016)

compounds (organic compounds, glycerol, trehalose, mannitol, arabitol, erythritol, etc.). In future, investigations on the extremophilic fungal genomes can be helpful to reveal the alteration in their cellular response in response to the extreme environment. Extremophiles that can survive in a wide range of harsh environments can further be used in a range of industrially important bioprocesses and in astrobiology studies.

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