Mechanistic Adaptation of Microbiomes in Extreme Environments

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Abstract

Extreme environments are referred to as ecosystems with a constant or fluctuating exposure to one or more environmental factors such as high and low temperatures, salinity, osmolarity, UV radiation, barometric pressure, and pH. Microbiomes inhabiting these ecosystems have vast and flexible metabolic diversity combined with extraordinary physiological abilities to colonize harsh environmental conditions. Extremophilic microbes offer a variety of adaptation strategies that include structural, physiological, and metabolic changes primarily in the cell membrane, DNA, RNA, protein, and enzymes. Adaptive strategies inevitably incorporate biological and geological processes such as pigment production, cell membrane changes, or movement into solid rock layers and geological modifications. In addition, the synthesis and accumulation of small molecules in the cytoplasm, surface modifications on proteins, for instance, acidification or increase in the stable amino acid content, molecular chaperones, polyphosphates, and mobile genetic elements also lead to better survival in hostile environments. Furthermore, characterisation of cell signalling systems in these populations, horizontal gene transfer, and transcriptomic and proteomic studies along with metabolomics may be especially useful in the analysis of the possibility of adaptations at group level. Owing to the enormous potential of commercial exploitation of extremophiles in biotechnology, understanding the processes underlying the adaptation of microbes to extreme environments from both evolutionary and ecological perspectives is of fundamental importance.

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3.1 Introduction

Extremophiles live in severe physical and geochemical environments that threaten life's physicochemical limitations such as high salinity, temperature, radiation, pH, desiccation, etc. This kind of harsh environmental conditions might be regarded as innate or induced factors which compel most living systems tough to survive and grow (Rothschild and Mancinelli 2001). Most of the genetic, bio, and physicochemical techniques that extremophilic microbes use are not fully explored so far. Apparently, nutritional requirements must be adapted to the availability at the particular extreme environment. Adaptation to physiological requirements may be complicated and diverse (Rampelotto 2013). Nevertheless, it was reported that some biological molecules and unusual biochemical strategies enable extremophiles to thrive, which garner great attention in the fields of biotechnology and other industrial processes.

Communication mechanisms (quorum sensing) used by these microorganisms in extreme environments are important for the survival of microorganisms (de Oliveira et al. 2015; Pérez-Rodríguez et al. 2015). Cell signalling controls many essential activities in microorganisms and can perform crucial tasks in managing diversity levels of microbes in extreme environments as well as ecological balance. Moreover, for synchronized expression of genes at elevated cell density, most bacteria rely on quorum sensing (QS) which is focused on the synthesis and recognition of autoinducer signalling molecules (Miller and Bassler 2001). Characterising cell signalling networks in these populations can present distinct ways to decipher the microbial communication associated with existence and functioning in intense climatic conditions. The most commonly reported signalling system is autoinducer-1 (AI-1) apart from thermophilic organisms since autoinducer-2 is present in them. Although peptide-based system was not common in this kind of microorganisms. Extremophiles use quorum sensing for processes such as cold adaptation, reduction of the freezing point and development of biofilms, tolerance to oxidative damage, and persistent cell development. Model organisms for all extremophile groups include *Leptospirillum ferriphilum* (acidophile) (Christel et al. 2018), *Sulfolobus solfataricus* (thermoacidophile) (Quehenberger et al. 2017), *Natronomonas pharaonis* (haloalkaliphile) (Falb et al. 2005), *Bacillus halodurans* (halophile) (Van-Thuoc et al. 2013), *Haloferax volcanii* DS2 (halophile) (Hartman et al. 2010), *Halobacterium* sp. NRC-1 (halo radiophile) (Berquist et al. 2007), *Deinococcus radiodurans* (radiophile) (Pavlopoulou et al. 2016), *Thermococcus barophilus* (piezophile) (Birien et al. 2018), *Halorubrum lacusprofundi* (psychrohalophile) (Liao et al. 2016), *Pseudoalteromonas haloplanktis* (psychrophile) (Parrilli et al. 2019), *Thermococcus kodakarensis* (thermophile) (Atomi and Reeve 2019), *Thermus thermophilus* (thermophile) (Miyazaki and Tomariguchi 2019), and *Cronobacter sakazakii* SP291 (xerophile) (Srikumar et al. 2019).

Extremophiles are crucial not only for their exceptional ability to survive extreme conditions but also for their wide range of uses in the areas of industrial and pharmaceutical biotechnology. Microbial communities were acclimatized to remarkable stress intensities in extreme conditions. These modifications play significant role in the improvement of remediation methods for certain polluted sites of hazardous waste and acid mine drainage sites. Novel enzymes isolated from extremophiles are tailored to extremes of temperature and pH. Lastly, they help in unravelling the evolutionary record as well as promising effects of climate in near future. Dynamic metabolic processes present in extremophiles were well explained by environmental transcriptomic and proteomic studies. Nonetheless, metabolic compounds explicitly associated with the microbial physiology are not fully explored. Due to the wide range of experimental complexities related to environmental matrix, metabolomic techniques fall behind other advanced technologies. The present chapter comprehensively discusses the basic microbial adaptations of various extremophiles for their survival.

3.2 Psychrophiles

At low temperatures, enzymes will be inactive, whereas solute concentrations are elevated and become lethal (Cavicchioli 2006). In addition, ice crystals can slice the cell membranes once the water is frozen, thereby damaging cell integrity (D'Amico et al. 2006). Psychrophilic membranes (*Shewanella putrefaciens*) contain increased amounts of unsaturated fatty acids, fatty acids with cyclopropane, and short-chain fatty acids that increase further with temperature reduction to modulate membrane fluidity (Feller and Gerday 2003; D'Amico et al. 2006; Gao et al. 2019) (Fig. 3.1). Psychrophilic microbes synthesize enzymes that are cold adapted and possess increased specific activities at cold conditions (Feller and Gerday 2003). Cold-tolerant enzymes can assist transcription and translation at very low temperatures. In addition, antifreeze proteins were found in microbes adapted to cold environments (Gilbert et al. 2004). AFPs have two major functions, namely thermal hysteresis and ice recrystallisation inhibition activity (Kawahara 2008). Such proteins can attach to ice crystals with a broad corresponding surface and thus avoid ice crystals from slicing the cell membranes.

Microorganisms have developed several physiological adaptations to balance the harmful impacts of cold environment such as producing temperature-related chaperones and antifreeze molecules, such as ice nucleation proteins (INPs), that shield the RNA and protein synthesis (De Maayer et al. 2014; Godin-Roulling et al. 2015). INPs arrest the extreme cooling of water due to ice crystallisation (Kawahara 2002; Muñoz et al. 2017). Psychrophiles control membrane fluidity by increasing the amount of branched-chain or unsaturated fatty acids or by reducing the stretch of fatty-acyl chains or both. Molecular chaperones help in protein refolding and have an

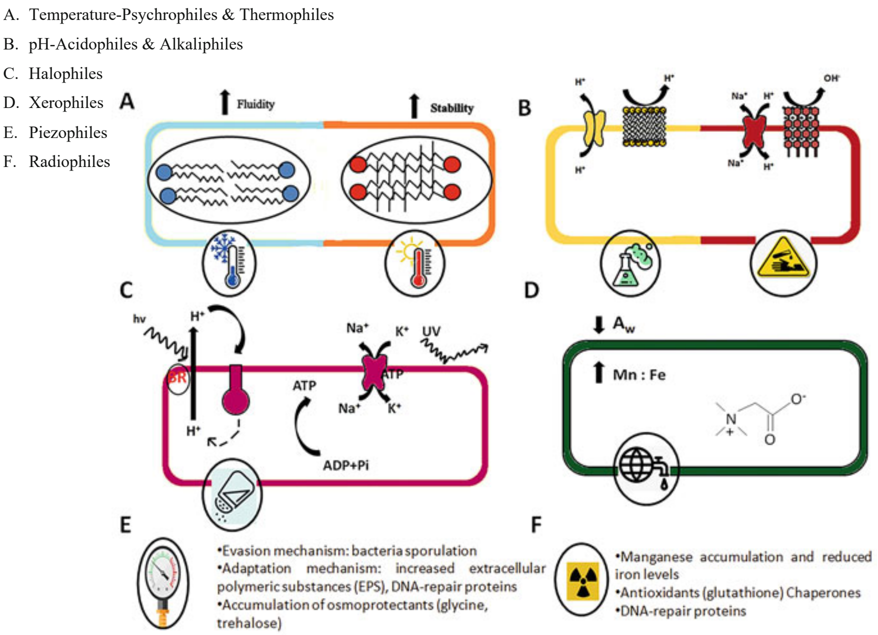

Fig. 3.1 Molecular mechanisms of extremophiles for their adaptation to extreme environmental conditions. (**a**) Temperature—psychrophiles and thermophiles. (**b**) pH—acidophiles and alkaliphiles. (**c**) Halophiles. (**d**) Xerophiles. (**e**) Piezophiles. (**f**) Radiophiles

effect on protein synthesis levels (Math et al. 2012). Prevention of UV damage to cells and reduction of cytoplasmic freezing point were achieved by aggregation of mannitol and other compatible solutes as cryoprotectants (Casanueva et al. 2010). In addition, they may probably stop protein assemblage/deterioration, stabilisation of membranes, and free radical scavenging in cold environment (Kandror et al. 2002) (Table 3.1).

The first bacterial AFP discovered from sea ice Gram-negative bacterium *Colwellia* strain SLW05 (Raymond et al. 2007). However, the earliest reported bacterial antifreeze characteristics were identified in soil bacterium *Rhodococcus erythropolis* and psychrophile *Micrococcus cryophilus* (Duman and Olsen 1993). Strikingly, *Pseudomonas fluorescens* KUAF-68 and *Pseudomonas borealis* DL7 have both ice nucleation and antifreeze activity (Kawahara et al. 2004; Wilson et al. 2006). Several types of ice nucleation proteins (i.e. InaK, InaQ, InaV, and InaZ) were reported in *Pseudomonas syringae* (Li et al. 2012). Temperature also affects structural proteins. To sustain their activities at low temperatures, enzymes have to surmount mainly two difficulties including cold distortion and slow reaction rates. Cold distortion takes place at freezing temperatures as they result in extra structured water molecules occupying the surface of protein resulting in less protein interaction and moving the system equilibrium towards the unfolded state (de Maayer et al. 2014). Other cold stress adaptations provided by EPS and cold shock proteins, in

Table. 3.1 Adaptations of extremophilic microorganisms under various climatic conditions

S. no	Type of extremophile	Microorganisms	Adaptation	Reference
1	Thermophiles	*Geobacillus* sp. TFV3	Chaperone protein DnaJ, chaperone protein DnaK, heat-shock protein GrpE, chaperone GroEL	Ching et al. (2020)
		Geobacillus, Parageobacillus	Heat-shock proteins (HSPs)	Wang et al. (2019)
		Geobacillus Thermodenitrificans ArzA-6, *Geobacillus toebii* ArzA-8 strains	EPS production	Panosyan et al. (2018)
		Thermolongibacillus, Aeribacillus, Geobacillus, Anoxybacillus	Biofilm formation	Cihan et al. (2017)
		Anoxybacillus sp. strain R4–33	EPS production	Zhao et al. (2014)
		Sulfolobus acidocaldarius, S. solfataricus, S. tokodaii	Biofilm formation	Koerdt et al. (2010)
2	Psychrophiles	*Paenisporosarcina Antarctica* CGMCC 1.6503^T	Fatty acid desaturases, dioxygenases, antifreeze proteins, and cold-shock proteins	Rong et al. (2020)
		Pseudoalteromonas sp. MER144	EPS production	Caruso et al. (2018)
		Colwellia psychrerythraea 34H	EPS production	Casillo et al. (2017)
		Pseudomonas mandelii	Alginate production, biofilm formation	Vásquez-Ponce et al. (2017)
		Flavobacterium frigoris PS1	Ice-binding protein (FfIBP)	Do et al. (2012)
		Pseudomonas syringae	Ice nucleation proteins (INPs) – Variant (InaQ)	Li et al. (2012)
		Sphingopyxis alaskensis	Polyhydroxyalkanoates (PHAs)	Ting et al. (2010)
		Pseudomonas putida GR12–2	Antifreeze protein (AfpA)	Muryoi et al. (2004)
		Colwellia strain SLW05	Antifreeze protein (AFP)	Raymond et al. (2007)
3	Halophiles	*Halomonas smyrnensis* K2	EPS production	Joulak et al. (2020)
		Alkalicoccus halolimnae BZ-SZ-XJ29^T	Ectoine biosynthesis gene cluster (ectA, ectB, and ectC)	Zhang et al. (2020a, b)

(continued)

Table. 3.1 (continued)

S. no	Type of extremophile	Microorganisms	Adaptation	Reference
		Nitriliruptoria species	K^+ influx and efflux, betaine and ectoine synthesis, and compatible solute transport	Chen et al. (2020a, b)
		Halomonas nitroreducens WB1	EPS production	Chikkanna et al. (2018)
		Salinibacter ruber	K^+ uptake via tropomyosin receptor kinase A	Oren (2002b)
		Methylarcula marina, M. terricola	Ectoine	Doronina et al. (2000)
		Halorhodospira Halochloris	Osmolyte glycine betaine	Galinski and Trüper (1982)
4	Acidophiles	*Acidithiobacillus caldus*	Ferric uptake regulator (AcFur)	Chen et al. (2020a, b)
		Acidithiobacillus ferrooxidans YNTRS-40	rus operon, res operon, petI, petII, sqr, doxDA, cydAB, and cyoABCD	Zhang et al. (2020a, b)
		Acidithiobacillus ferrooxidans	Proteins associated with inorganic sulphur compound (ISC) oxidation	Bellenberg et al. (2019)
		Acidithiobacillus ferrooxidans	Fumarate nitrate reduction transcription factor (FNR)-like protein (FNR_{AF})	Osorio et al. (2019)
		Acidithiobacillus	Squalene–hopene cyclase (SHC) sequences	Jones et al. (2012)
		Picrophilus torridus	Potassium-transporting ATPases and other cation transporter	Fütterer et al. (2004)
		Ferroplasma Type II, *Leptospirillum* group II (*L. ferriphilum*)	Proton efflux systems (H^+ ATPases, antiporters, and symporters)	Tyson et al. (2004)
		Ferroplasma acidarmanus	Tetraether-linked membrane monolayers	Macalady et al. (2004)
5	Alkaliphiles	*Bacillus* sp. AK13	EPS production	Jung et al. (2020)
		Alcaligenes sp., *Dietzia* sp.	Biofilm formation	Rout et al. (2018)
		Alishewanella, Dietzia spp.	Biofilm formation	Charles et al. (2017)
		Cronobacter sakazakii	EPS production	Jain et al. (2012)

(continued)

Table. 3.1 (continued)

S. no	Type of extremophile	Microorganisms	Adaptation	Reference
		Vagococcus carniphilus MCM B-1018	EPS production	Joshi and Kanekar (2011)
		Bacillus pseudofirmus OF4	Plasmids, cardiolipin synthase genes, sodium-coupled Npt type phosphate transporters, toxin-antitoxin genes mazE mazF	Janto et al. (2011)
		Thioalkalimicrobium aerophilum strain AL 3^T, *Thioalkalivibrio versutus* strain ALJ 15	Accumulation of unsaturated fatty acids, cyclopropane fatty acids, organic compatible solutes, pigments	Banciu et al. (2005)
6	Piezophiles	*Salinimonas sediminis* N102T	tesA (acyl-CoA thioesterase I), tesB (acyl-CoA thioesterase II), and yciA (acyl-CoA thioesterase YciA); polyhydroxyalkanoates, rRNA operons	Xue et al. (2020)
		Colwellia	More basic and hydrophobic proteome, archaeal methyltransferase for tRNA modification, NADH ubiquinone oxidoreductase (nuo) gene cluster	Peoples et al. (2020)
		Shewanella benthica DB21MT-2	Toxin-antitoxin (TA) system	Zhang et al. (2019)
		Thermococcus barophilus	Mannosyl-glycerate (MG)	Cario et al. (2016)
		Thermococcus piezophilus $CDGS^T$	Synthesis of compatible solutes, several hydrogenase gene clusters (hydrogenases and sulfhydrogenases)	Dalmasso et al. (2016)
		Photobacterium profundum SS9	Monounsaturated fatty acid accumulation	Allen et al. (1999)
7	Radiophiles	*Deinococcus radiodurans*	Single-stranded binding proteins (DdrB and SSB)	Lockhart and DeVeaux (2013)
		Rubrobacter xylanophilus, *Rubrobacter radiotolerans*	High intracellular concentration of trehalose, Mn^{2+}	Webb and DiRuggiero (2012)

(continued)

Table. 3.1 (continued)

S. no	Type of extremophile	Microorganisms	Adaptation	Reference
		Deinococcus radiodurans	Nucleotide excision repair pathway (uvrA1B), base excision repair pathway (ung and mutY), homologous recombination pathway (recA, ruvA, ddrA, and pprA)	Makarova et al. (2001)
8	Xerophiles	*Helicobacter pylori*	Serine protease HtrA	Zarzecka et al. (2019)
		Actinopolyspora, Nocardiopsis, Saccharomonospora, Streptomonospora, Saccharopolyspora	Polyketide synthetases and non-ribosomal peptide synthetases (NRPS)	Meklat et al. (2011)
		Nostoc commune	Water stress proteins (WSP)	Gao and Ye (2007)
		Caulobacter crescentus	Chaperone systems (DnaK/DnaJ and GroES/GroEL)	Susin et al. (2006)

addition to extensive microbial decomposition and nutrient reuse potential, are also documented for microbial mat communities from ice layers of Antarctica and the Canadian High Arctic (Varin et al. 2012).

3.3 Thermophiles

The molecular mechanisms of microbial adaptations to temperature extremes were thoroughly investigated in comparison with other conditions. Enzymes denature at elevated temperatures, become inactive, and, thus, hinder the metabolic activities. Besides, increase in the membrane fluidity takes place disrupting the cell. The thermophilic microbes possess a wide range of cell modifications to avoid cell disruption. Thermophilic membrane lipids include more saturated fatty acids and straight-chain fatty acids than mesophilic organisms (15–40 °C) (Reed et al. 2013) (Fig. 3.1). These features allow thermophiles to sustain elevated temperatures and maintain membrane integrity. Improved stability of proteins isolated from thermophiles was attributed to their more basic nature and small size (Kumar and Nussinov 2001).

In addition, monovalent and divalent salts improve nucleic acid stability since they conceal the negative charges. DNA will be protected from depuration and hydrolysis by the presence of phosphate groups, KCl and $MgCl_2$ (Hickey and Singer 2004). Another way of stabilising DNA is by using DNA-binding proteins and by compression of whole genome into chromatin (Marguet and Forterre 1998). A common mode of thermophilic microbes to protect their cell machinery at extreme temperatures is the adaptation of these proteins by modifying the primary structure amino acid composition, thus enhancing their thermal stability (Xu et al. 2018). Proteins of thermophiles have a greater proportion of short length amino acids as well as α-helices containing amino acid residues (Urbieta et al. 2015; Xu et al. 2018). Another main strategy is the presence of heat-shock proteins (HSPs), like DnaK, GroEL, and GroES chaperones in protein folding. In a recent study by Wang et al. (2019), stress-tolerant HSP genes from thermophiles *Geobacillus* and *Parageobacillus* were isolated which contributed to the increased heat and osmotic tolerance. In addition, DNA damage is effectively handled by DNA-repair systems (SOS system). They use fatty acids arranged in branched chains and polyamines (spermidine) to stabilize the membranes. Another adaptation employs the suitable solutes to stabilize cellular components (Urbieta et al. 2015). Furthermore, proteins from the glycolysis pathway (pyruvate dehydrogenase complex) supply instant energy to survive the high-temperature stress conditions (Wang et al. 2015) (Table 3.1).

Additional hydrogen bond networks, reduced surface loop length, enhanced secondary structure tendency, increased core hydrophobic nature, improved Van der Waals interactions, ionic exchanges, and better packing density, on the whole, contributed to thermal stability of protein (Brininger et al. 2018). More recently, it has been shown that cells of archaea use a structure stabilisation strategy along with aforementioned adaptations, whereas bacterial cells utilize a sequence stabilisation strategy (Berezovsky and Shakhnovich 2005). The lipid composition of the thermophilic membranes is yet another well-known adaptation. Some species have novel/specific lipids, such as *Thermotoga maritima* (15,16-dimethyl-30-glyceryloxtriacontanedioic acid) (Siliakus et al. 2017). In archaea, ether-based lipids were found to be hydrolysis-resistant at high temperatures. In contrast, cells of archaeal thermophiles comprise a monolayer consisting of “fused lipid bilayer”, which was shown to be resistant for hydrolysis at higher temperatures (DasSarma et al. 2009).

In thermophiles, DNA shows thermal resistance by inserting positive supertwists by reverse gyrase (Jamroze et al. 2014). In addition, an increase in GC base pairs has been shown to stabilize DNA in specific regions (stem-loops). Thermophilic archaea contain histones directly correlated to the eukaryotic core histones (H2A/B, H3, and H4). Binding of these histones was demonstrated to enhance DNA melting temperature (Stetter 1999). Besides, specific microbial adaptations to improve protein stability at extreme temperatures comprise a greater number of disulphide bridges, improved aromatic peptide interactions, and enhanced peptide hydrogen bonding (Maier and Neilson 2015).

3.4 Acidophiles

Acidic pH conditions are a threat to cellular biochemistry, as extreme low pH contributes to protein degradation. Acidophilic microbes preserve their proteins by adding additional amino acids with neutral side groups and aggressively pumping protons out of the cell to preserve steady intracellular pH conditions (Baker-Austin and Dopson 2007). They possess a complex of cell modifications to control pH within the cell. Many exoenzymes are reported to be efficient at very low pH than the pH of cytoplasm which is isolated from acidophiles. In addition to these enzymes, other significant biomolecules like plasmids, rusticynin, and maltose-binding proteins were isolated from acidophiles.

Acidophiles have many distinguishing structural and functional features for pH control (Golyshina et al. 2000; Crossman et al. 2004). Although these species are able to live under extremely acidic conditions, they do not withstand this kind of circumstances within the cell since DNA turns uncertain; hence, they have established strategies for pumping acid out of the cell to keep neutral to weak acidic environment (pH 5–7) within the cell (Matin 1999). Furthermore, some records of several other species with acidic internal pH (Van de Vossenberg et al. 1998; Macalady et al. 2004). Other proton flux systems include primary proton pumps (symporter) and secondary proton pumps (e.g. antiporter cation/HC), as well as proton-consuming reactions. *Leptospirillum ferriphilum* was shown to contain a carbonic anhydrase and amino acid decarboxylases which assist in pH equilibrium by overwhelming protons (Christel et al. 2018). Next strategy is a reduced cell membrane permeability which suppresses the cytoplasmic proton entry. The entry of protons is constrained by KC ions produced within positive membrane potential (Christel et al. 2018). In *Leptospirillum ferriphilum,* a broad range of genes associated with biosynthesis of cell membrane has been identified that can be related with acid tolerance.

Adaptations comprise a cell membrane that is relatively proton-impermeable (Konings et al. 2002). Another mechanism is the reduced pore size of membrane channel which was demonstrated for *Acidithiobacillus ferrooxidans* (Amaro et al. 1991). Acidophilic microbes comprise net positive charge within the cell which can offset the elevated H^+ ion concentration in their environment. They can use aggressive proton pumping, as reported in *Bacillus* and *Termoplasma* (Michels and Bakker 1985) (Fig. 3.1). Microbes should preserve a near-neutral cytoplasmic pH to allow cellular activities for their growth and metabolism (Krulwich et al. 2011; Jin and Kirk 2018). One of the first functions to evolve inside the earliest cells was possibly the balance of protons through various transporters, together with the ion-using ATP synthase (Lane and Martin 2012). Chemiosmosis is also a feature of both bacterial and archaeal cells (Lane et al. 2010).

Acidophiles may discharge organic metabolites like acetic acid and lactic acid in addition to intracellular pH, thereby modifying the nearby pH conditions (Zhang et al. 2016). Many of them consist of organic acid degradation pathways to avoid proton separation by organic acids (Baker-Austin and Dopson 2007). Archaeal members like *Ferroplasma acidiphilum* and *Sulfolobus solfataricus* were reported to contain tetrapetric lipids in the cell membrane which offer resistance to acidic pH. Advanced protein and DNA-repair systems were found in acidophiles compared to mesophiles. A pH shift from 3.5 to 1.5 externally persuades the proteins concerned with heat-shock reaction, for instance, chaperones were reported in *Acidithiobacillus ferrooxidans* (Amaro et al. 1991).

In a study conducted by Guazzaroni et al. (2013), novel acid resistance genes from the metagenome of the Rio Tinto River were isolated including ClpXP protease, the transcriptional repressor LexA, and nucleic acid-binding proteins such as an RNA-binding protein, HU, and Dps (Table 3.1).

3.5 Alkaliphiles

Under alkaline conditions, H^+ concentrations are particularly low and cells experience trouble using ATP synthase to generate energy and precipitation of other essential ions like Mg^{2+} and Ca^{2+} from water as salts will take place (Krulwich et al. 1998). Alkaliphiles overcome these complexities by vigorously pumping in these ions and by transporting others to preserve neutral conditions. Besides, the cell wall of alkaliphiles serves as a protective shield to harsh climatic conditions (Horikoshi 2006) (Table 3.1). Alkaliphilic microbes have evolved a cell wall with negative charge, lowering the environmental pH external to the cell. They also synthesize an additional acid cell wall consisting of teichurono-peptide and teichuronic acid or polyglutamic acid. All these acids absorb H^+ and resist OH^- and probably assist in generating the proton motive force required to stimulate the synthesis of ATP. The proton motive force for ATP synthesis is driven by Na^+ or K^+ antiporters in several alkaliphilic *Bacillus* species, which catalyses an electrogenic swapping of external ions (Na^+ or K^+) and high number of entries into H^+ ions (Preiss et al. 2015). In general, alkaliphiles can use these antiporters (Na^+/H^+ and K^+/H^+) (Krulwich et al. 2011) and also generate acids to lower the inner pH when metabolism is impaired due to elevated pH levels (Moran-Reyna and Coker 2014). The transporters are regulated, possibly through a transmembrane pH sensor signalling (Krulwich 1995) (Fig. 3.1).

3.6 Halophiles

Increased salt concentrations usually deprive protein water content leading to accumulation and precipitation due to exposed hydrophobic patches binding to one another. To neutralize this, these microbes have formed a proteome consisting mostly of acidic proteins (Brininger et al. 2018), and the acid remnants (aspartic & glutamic acid) are usually located on the protein surface. They help in arranging the water molecules (H^+ of water interacts with COO^- of acidic side chain) surrounding proteins building a “water cage” which guards the proteins from dehydration and precipitation (DasSarma and DasSarma 2015; DasSarma et al. 2009).

Many halophiles retain increased concentrations of various solutes in their cytoplasm in response to the salt to maintain their interiors in osmotic equilibrium with the external world. *Halophilic archaea* maintains exceptionally high KCl in its cells (Oren 2002a, b). Halophilic proteins must be properly folded and operative in heavy salt concentrations considerably similar to the hyperthermophilic proteins which stay functional around 100 °C (Michael et al. 1999). Halophiles achieve the necessary osmotic balance by accumulating KC in the cytoplasm as a “salt-in” strategy and combined action on bacteriorhodopsin and ATP synthase (Margesin and Schinner 2001). Other strategy observed was the exclusion of salts through the synthesis of suitable organic solutes like polyols, amino acids, sugars, and betaines. The “salt-in” strategy has only been established in a small number of halophilic microbes (e.g. *Salinibacter* and *Halanaerobiales*) that need KCl to form active proteins (Fig. 3.1). On the contrary, various halophiles using salt omission approach can withstand a variety of salt concentrations because of the synthesis of organic solutes to counteract the high salt content in the surroundings (Oren 2013). Many microorganisms need to adapt to low water activity in saline environments. It was established that freezing point of water can be considerably decreased by salts; however, solutions containing saturated salts show very low water activity. Apart from pH and salinity, water activity is the only variable that certain microbes are able to control using their metabolites capable of accumulating or captivating water (e.g. EPS proteins and polysaccharides) (Frösler et al. 2017).

Halobacillus halophilus, isolated from a salt marsh on the North Sea coast of Germany, can withstand high levels of salt content up to 3.0 M NaCl with an optimum survival rate of 38% (Roeßler and Müller 1998). *H. halophilus* adopts a hybrid osmoadaptation approach by collecting together molar chloride concentrations and suitable solutes (glutamate, glutamine, proline, ectoine, N-acetyl ornithine, and N-acetyl lysine) (Saum et al. 2013; Saum and Müller 2008). More recently, *Halomonas socia* strain CKY01 developed polyhydroxybutyrate (PHB) with genes responsible for the absorption, synthesis, and transportation of osmolytes such as betaine, choline, ectoine, carnitine, and proline as a strategy for survival (Park et al. 2020) (Table 3.1).

3.7 Xero-Tolerant Extremophiles and Oxidative Stress

Xerophiles are able to sustain in dry climatic conditions with water activity <0.75 (Connon et al. 2007; Lebre et al. 2017). Additional parameters like hot and cold temperatures, poor water activity, increased salt concentrations, poor organic carbon content, and extreme radiation, in addition to low rainfall, intensify xeric conditions, limiting existence of microbes (Dose et al. 2001; Crits-Christoph et al. 2013). Xerophiles have evolved few survival mechanisms in dry environments including environmental stress avoidance and adaptive mechanisms (Table 3.1). Avoidance of dry environment requires alteration of cells into non-replicative viable state by development of spores (Crits-Christoph et al. 2013). Adaptive strategies are related to the prevention of water loss and improved water preservation by amassing of osmoprotectants (trehalose, L-glutamate, glycine betaine), synthesis of EPS, cell membrane alterations to maintain intracellular water, DNA repair, and protein synthesis (Dose et al. 2001; Lebre et al. 2017) (Fig. 3.1). Under oxidative stress, proteins undergo conformational changes that contribute to the unfolding and aggregation of proteins. The key drivers of protein folding are DnaK and GroEL chaperones along with other cochaperones that stabilize proteins by promoting adequate folding and preventing their self-association (Susin et al. 2006).

Desiccation tolerance is distinctive in the midst of other extreme conditions faced by microbes since the cells will not proliferate under desiccation and most of their lifespan might be used up in desiccated condition. Therefore, desiccation cycles tend to persuade survival mechanisms for the cells instead of the capability to survive under harsh conditions. As stated by Maier and Neilson (2015), well-established survival mechanisms consist of DNA protection and repair ability when exposed to UV radiation, maintaining protein stability during desiccation and preserving membrane integrity. The main survival strategy of cyanobacteria is the synthesis of EPS which controls water absorption and loss, acts as a matrix for the immobilisation of cell contents formed by cell in reaction to dehydration, and possibly shields cell walls during shrinking and swelling (Potts 1999). EPS facilitates the formation of biofilms and may be essential components of water loss prevention mechanism that seals the cell (Ortega-Morales et al. 2001). When exposed to desiccation and UV stress, the cell produces multiple molecules. They were also reported in EPS and contain UV captivating molecules such as mycosporine-like amino acids and scytonemin, carotenoids, and detoxifying enzymes or radical quenchers that defend against harsh radicals, oxygen species, and water stress proteins (WSP) (Gao and Ye 2007). WSP were found to be highly stable, and up to 70% of the soluble proteins are present in *Nostoc commune*. Additionally *N. commune* cells contain trehalose and sucrose, which are capable of stabilising proteins and maintain membrane integrity during desiccation (Maier and Neilson 2015). In pathogens like *Helicobacter pylori*, serine protease HtrA plays key role in survival under various stress conditions (thermal, osmotic and acidic) (Zarzecka et al. 2019) (Table 3.1).

3.8 Piezophiles

As the pressure increases, membranes lose fluidity and permeability since lipids arrange themselves more compactly and reach a thickening process similar to what occurs at extremely low temperatures (Bartlett 2002). Organisms avoid this problem by increasing the proportion of polyunsaturated and monounsaturated fatty acids or phosphatidylglycerol and phosphatidylcholine in their membranes, rather than phosphatidylethanolamine (Usui et al. 2012; Siliakus et al. 2017) (Table 3.1). Protein-protein interactions are responsive to high pressure leading to the dissociation of enzymes (Sharma et al. 2002). Pressure is known to modify gene expression (Nakasone et al. 1998). Further modifications may contain chaperone-encoding genes for upregulation, respiratory chain alteration, porin expression, and development of osmolytes (Oger and Jebbar 2010; Jebbar et al. 2015) (Fig. 3.1).

3.9 Radiophiles

When bacteria are exposed to perils of environmental stress as ionising (gamma) radiation and UV radiation, a series of signals were expected to trigger physiological responses. Ionising radiation is primarily accountable for double-stranded breaks in microbial genome. On the other hand, both proteins and lipids will also get damaged, and constant oxidative stress was induced upon exposure (Slade and Radman 2011). Consequently, ionising radioresistant microbes developed unique strategies like new and robust DNA repair mechanisms, antioxidant and enzymatic defence systems, and a condensed nucleoid. Rapid and effective genome repair is important for sustaining ionising radiation doses. This was demonstrated by the use of the nucleotide excision repair pathway (uvrA1B), base excision repair pathway (ung and mutY), and homologous recombination pathway (recA, ruvA, ddrA, and pprA) in *Deinococcus radiodurans* (Makarova et al. 2001). In *Halobacterium* sp. NRC-1 (genes close to Rfa) (Berquist et al. 2007) and *D. radiodurans* (DdrB and SSB) single-stranded binding proteins were reported (Cox et al. 2010; Lockhart and DeVeaux 2013; Pavlopoulou et al. 2016). The cells of *D. radiodurans* consist of many of the following mechanisms for preventing oxidative stress and resistance. The cell cleans up by removing oxidized macromolecules, selective protein defence versus oxidative injuries, and the inhibition of reactive oxygen output. It has also been shown that a condensed nucleoid facilitates the efficiency/accuracy of DNA repair (Minsky et al. 2006) and restricts the diffusion of radiation-generated DNA fragments (Daly et al. 2007).

UV radiation enhances reactive oxygen species (ROS) production, with two distinct outcomes. Initially, ROS acts as cell signals encouraging cells to defend themselves against these stressors (Caldwell et al. 2007), and later when ROS levels exceed the cell's defence mechanisms, significant cell damage and apoptosis may occur. Biofilm formation is one of the techniques formed by microorganisms to colonize areas with high levels of UV radiation. Biofilms are layers of planktonic bacteria attached to each other, forming an intricate, growing, three-dimensional structure at their surfaces. Bacteria need to communicate with each other (quorum sensing) to develop this three-dimensional colony, and polyP was proposed as the modulator of quorum sensing and development of biofilms. UV radiation subtly damages DNA through the formation of cyclobutene pyrimidine dimmers (thymine dimers) and pyrimidine-pyrimidone (6–4) photoproducts (6–4 PPs). They account for approximately 80% of photolesions induced by UV radiation (Jones and Baxter 2017) (Table 3.1).

Radiophiles generally exploit an amalgamation of photoreactivation (phr) genes, nucleotide excision repair (uvrABCD, xpf, and rad), base excision repair (mutY and nth), and homologous recombination (recA and radA/51) to restore these DNA lesions (Jones and Baxter 2017). In addition, microbes have developed a set of photoprotective strategies to defend themselves from continuous exposure to UV radiation. They incorporate carotenoids, gene duplication via polyploidy, genome composition hydroperoxidases and superoxide dismutases (Jones and Baxter 2017), effective DNA-repair machinery, chaperone induction, and dynamic protection against oxidative stress induced by UV radiation (e.g. accumulation of glutathione) (Pérez et al. 2017). Radiation resistance has been correlated with the ability of these microorganisms to repair DNA damage, because it was reported that radiophiles aggregate elevated levels of intracellular Mn^{2+} and reduced Fe (Pikuta et al. 2007) bestowing UV radiation resistance (Paulino-Lima et al. 2016) (Fig. 3.1).

3.10 Conclusions and Future Perspectives

Life on Earth will continue to be found in a plethora of climatic conditions previously considered to be adamant from an anthropocentric viewpoint to sustain existence of life. Studying extreme environments and extremophile biology including their position will help in predicting and hypothesising theories about situations that prevailed in the course of origin and progression of life on the ground and throughout the world. In the midst of rapid innovations made over the past few decades and latest developments in “omics” tools, extremophilic world has been thoroughly investigated, and our understanding of biosphere was evolved, extending the limits of life on Earth. Extremophiles take part in many important tasks in the environment. Their robust nature to resist, sustain, and mediate catalysts under harsh environmental conditions not only make them exceptional but also promising for environmental conservation. Extremophiles like deep-sea microorganisms contribute greatly to the atmospheric geochemical cycles. They preserve the chemical equilibrium in the environment, help to lessen the greenhouse gases (GHGs) in the atmosphere, and detoxify the hazardous chemicals in the environment. Next-generation sequencing (NGS) and next-generation proteomics (NGPs) provide important strategies for gaining insight into the molecular processes concerned with extremophilic strategies for survival (Armengaud 2016). This kind of research and methodologies may illustrate the strategies that microorganisms use to acclimatize to harsh climatic conditions and are constructive in understanding the microbial evolution with respect to extreme environments.

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