

Review

Desiccation tolerance in cyanobacteria

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All abiotic stresses adversely affect growth and development of cells. Direct effect of these factors results into condensation of nucleoid, crowding of cytoplasmic components, and increase in the T_m of membrane phase transition. Cells under prolonged exposure to these stresses, show pronounced effect on proteins, nucleic acids, and lipid membranes. Those that have developed mechanisms for acclimation only survive under unfavorable conditions. Bound water in both proteins and nucleic acids plays extensive role in tolerance to stress. Water stress proteins are most abundant proteins, in cyanobacteria, accumulated in extracellular glycan sheath and releases during desiccation. Besides these, Histones-like DNA binding proteins maintain nucleoid organization and regulate DNA repair. Certain special enzymes "Repair Ligases" also provide tolerance to bacterial cells, under stress conditions especially desiccation. Number of chromosome copies per cell is also important to this act the lethal effect of stress. Membrane fluidity plays important role in temperature perception, which is mediated by Histidine Kinases, localized in plasma membrane. Fatty acid desaturases (enzyme) enhance degree of unsaturation of fatty acids in the plasma membrane that is inducing double bonds in fatty acids, as a consequence of which *Des A* gene is expressed (in low temperature stress). Cyanobacteria accumulate compatible solutes in response to increases external salinity. Tolerance increases from sucrose or trehalose to glucosylglycerol and glycinebetamine accumulating species. Na^+/H^+ antiporters are responsible for salt and pH regulation in *Synechocystis*. The present review combines and compares all the abiotic stress mechanisms including desiccation, temperature, pH and salinity. It also underlines the common mechanistic pathways in all the stress operating in cyanobacteria as well as highlights the signaling molecules that play pivot role in tolerance for stress and that are common in different mechanisms.

Key words: Cyanobacteria, desiccation, tolerance, mechanism, proteins, nucleic acids, membranes.

INTRODUCTION

Cyanobacteria are a diverse group of prokaryotes known also as blue-green algae. They are either unicellular or filamentous, and perform plant-type oxygen-evolving photosynthesis. They are known to inhabit a variety of sea, freshwater and terrestrial habitats, and show many responses to changes in milieu exterior. Cyanobacteria dominate the bacterial populations of many extreme environments (Whitton and Potts, 1999) such as deserts (Palmer and Friedmann, 1990; De Chazal et al., 1992), thermal springs (Ward et al., 1989), hot brines (Dor and Paz, 1989), frigid lakes (Orcutt et al., 1986), soda lakes (Ciferri, 1983) and the nutrient-poor open ocean (Kevin Sellner, 1997). The one that experience extremes of desiccation include intertidal marine mats, often dominated by a form species of *Microcoleus* (Pentecost, 1985; Potts, 1977; Potts and Whitton, 1977, 1980), growths of *Gloeocapsa* in tinstenrich communities, and terrestrial

crusts of *Tolypothrix*, *Calothrix* and *Nostoc* (Whitton et al., 1979; Potts and Whitton, 1980; Whitton, 1992; Amarpalli et al., 1997; Tripathi et al., 1997). A huge diversity of cyanobacteria is known to occur in hot (Bhatnagar and Bhatnagar, 2005) and cold deserts (W. Williams) where the single most important factor that affects their growth is unavailability of water. Desiccation in general is the consequence of either no or negligible precipitation and /or high or freezing temperature. On the other hand loss of water during desiccation increases concentration of salts around the organism/cell that may leads to plasmolytic situations. High salt concentrations in turn causes rise in pH. Radiations too play havoc under frozen conditions and tropical heat. Thus one easily visualize that these stresses in nature often occur simultaneously. Therefore it is imperative that survival under stress will mean certain general themes to sense stress and also to

impart tolerance.

Low precipitation, prolonged drought and thermal stress (-20 to +40°C) are the factors that create desiccated conditions. Another important factor is metric water potential. Water potential (Ψ) is the difference in the free energy between the system and pure water at the same temperature. *Crinalium episammum* survives a water potential of -400 MPa. *Nostoc* can tolerate and survive when exposed to -100 MPa in desert environment (De Winder, 1990; Potts, 1997 unpublished cited in Potts, 1994). *Chroococcus* and *Chroococidiopsis* can tolerate Ψ below -3MPa (Potts and Friedmann, 1981). Mean lowest Ψ recorded in Antarctic endolithic is -66 MPa (Nienow and Friedmann, 1993), while in hot deserts cyanobacteria dominated by *Chroococidiopsis* Ψ recorded is -6.9 MPa (Palmer and friedmann, 1990). In hot crust, *Microcoleus societus* are partially inactive at -0.7 MPa and completely inactive at -1.8 MPa (Brock, 1975).

EFFECTS OF STRESS FACTORS ON

Nucleic acids

Desiccation leads to accumulation of mutations (damage) time, when there is no cell growth. Damage to DNA may arise, due to chemical modifications (alkylation and oxidation), crosslinking, and base removal such as ionizing and non-ionizing radiations. Single stranded breaks occur on desiccation. DNA undergoes appreciable light dependent nicking after only short period of time, while cells are dried in air (Stulp and Potts, 1987). Conformational changes in DNA are influenced by hydrophobic interaction in the major groove of DNA as a result of base methylation (Potts, 1994). Low water activity (a_w) is responsible for causing conformational changes in DNA converting it from B to A form (Potts, 1994).

The immobilization and rapid drying of cells (*Nostoc* UTEX 584), leads to rapid loss of $rpoC_1C_2$ transcript, encodes two subunits (β, β') of the RNA polymerase. Alteration may arise, because of increase in covalent cross-linking between proteins and DNA that accumulate continuously during desiccation, the so-called Maillard or Browning reaction (Figure 4).

Ultraviolet (UV) damage to DNA appears to depend on the secondary structure of the double helix, which is further influenced by amount of bound water (Potts, 1994) and apparently the availability of water (Potts, 1994, 99). Desiccation ultimately causes loss of control mechanism that maintains low reactive oxygen species concentration (Kranner, 2002; Kranner et al., 2002). Resulting increase in loss in active oxygen leads to deteriorative process such as aging and eventually death (Harman, 1956, 87; Beckmann and Ames, 1998). Highly reactive molecules such as ROS are the most prominent source of damage to nucleic acids. The OH radical can

attack and even damage almost every molecule found in a living cell. It can, for example, hydroxylate purines and pyrimidines bases in DNA (Halliwell, 1987), thus enhancing mutation rates.

Proteins

According to Potts (1994) as the cell dried and then desiccated, the total turn over of proteins is represented by K_{cat} value. This K_{cat} value tends to have less meaning as cell enters a period of quiescence that may last for years. Modified proteins represent considerable fraction of protein pool on cell rehydration. The number of water molecules (bound water) in a cell micro environment, influence the equilibria between the different intermediates of folding pathway of each proteins. Water is necessary for protein structure and folding (Potts, 1999).

Damage to proteins is mediated through reactive oxygen species. Oxidative damage to proteins changes their configuration, mostly by oxidizing the free thiol residues of cystein to produce thiyl radicals. These can form disulphide bonds with other thiyl radicals, causing intra- or inter-molecular cross-links. Desiccated cells of cyanobacteria, do infact contains appreciable amount of free radicals. Oxidative damage will be manifest in proteins, leading to loss of a diffusion barrier to membranes- impermeable markers and ultimately to cell lysis (Potts, 1994). Proteins become sensitive to proteolysis, inactivated and show reduced activity. Univalent reduction of oxygen produces O_2^- , H_2O_2 and OH^- and show following redox potential (Figure 5) converted to asperginylyl, pyroglutanyl aldehyde and methionyl sulfate residue (Potts, 1994). At low temperature protein denaturation occurs (Guy et al., 1998) (Table 1).

Lipid membranes

Under temperature stress, membrane without trehalose undergoes vesicle fusion, changes in morphology and loss of calcium transport activity. Upon subsequent rehydration (Crowe et al., 1992) rapid increase in membrane fluidity occurs, induced by direct physical effect of the temperature upshift (Meija et al., 1995; Dynlacht and Fox, 1992). Degree of saturation of fatty acids of plasma membrane and change in membrane fluidity is an ultimate result of low temperature stress.

Reactive oxygen species play a role in generation of membrane damage (Mc kersie and Bowlef, 1997). Cyanobacteria can tolerate maximum of 0.5 M NaCl, low Na^+ concentration is essential for cyanobacteria to survive, while hypersaline strains can tolerate up to 3 M NaCl. At high salt concentration, cyanobacteria actively extrude Na^+ and accumulate K^+ and maintain internal ion concentration (Reed et al., 1985) (Figure 1).

Table 1. Water stress proteins and heat shock proteins: A comparison of mode of action.

S/No.	Water stress proteins	Heat shock proteins
1	Three Wsp polypeptides 32, 37 and 39 kDa appear to be isoforms, accumulate in the extracellular glycan, and show homologies with carbohydrate-modifying enzymes (Hill et al., 1994a).	Heat shock proteins, by definition, are induced by a heat shock, that is, a transient increase in temperature enhances the expression level of chaperones and co-chaperones (Grimshaw, Jhon. P. et al., 2003)
2	Associated with 1,4- <i>b</i> -D-xylanxylohydrolase (EC 3.2.1.8) activity and play role in the modification of the extracellular glycan which contains xylose (Helm and Potts, unpublished).	Hsp are located in plasma membrane or in cytosol. 24 putative hsp genes are identified in <i>Synechocystis</i> (Suzuki et al., 2000)
3	Water stress proteins ' (Wsp) have a structural role in cell stability in view of their abundance and their high content of hydroxylated amino acids (serine, threonine and tyrosine).	Proteins of four size classes (70, 60, 17, and 14 kDa) were induced when <i>Synechocystis</i> cells had been subjected to HS (Horvath et al., 1998).
4	Wsp polypeptides, and UV-absorbing pigments, form complexes in the absence of salt, exist in a monomeric state in the presence of salt (Hill et al., 1994a). Ionic interactions attenuated <i>in situ</i> through drying and wetting of colonies and the resultant changes in salt concentration (Potts, 1999).	HSP17 is thylakoid-associated during HS, also membrane bound under thermal stress. Chaperonin, associated with unilamellar vesicles and stabilized the membrane at high temperature by increasing its microviscosity, retained the incapability to assist protein folding. Though the exact function of HSP17 protein in <i>Synechocystis</i> is hitherto unknown (Horvath et al., 1998).
5		Recently, two additional <i>dnaK</i> (homologues as found in bacteria) have been revealed in the <i>Synechocystis</i> genome. The <i>groESL</i> operon and the <i>cpn60</i> gene possessing no <i>groES</i> in the neighboring region encode the HSP60 proteins. HSP14 was identified as <i>groES</i> , the cochaperonin of <i>GroEL</i> (Horvath et al., 1998).
6		Various cold-inducible genes have been identified in cyanobacteria, genes for fatty acid desaturases, RNA-binding proteins, ribosomal protein S21, ribosomal protein L9, cytochrome CM and two RNA helicases. The roles of proteins encoded by low temperature inducible genes in the acclimation to low temperature are not fully understood (Murata and Suzuki, 2001).
7		Function of HSPs is in folding of nascent proteins and refolding of denatured proteins (Horvath et al., 1998).

MECHANISM OF TOLERANCE

Varied number of mechanism for tolerance to these abiotic stresses, are present in cyanobacteria. Firstly, water content of desiccated *Nostoc* cell is approximately one order of magnitude lower than that of cyanobacterial akinetes. Secondly the consequence of drying or equilibrium of cells in an atmosphere of controlled water potential is fundamentally different from those that result from placing cell in a solution of a given solute. Third, cells may use compatible solutes to regulate their

intercellular water potential during osmotic stress but not desiccation stress (Potts, 1994; Record et al., 1998).

Nucleic acids

A mechanism is present to retard the rate of depurination and other DNA damage. As the temperature increases, depurination rate increases. *Nostoc commune* genome contains significant amount of 6 methyladenine, these residue lost from DNA 2-3 times faster than other purines

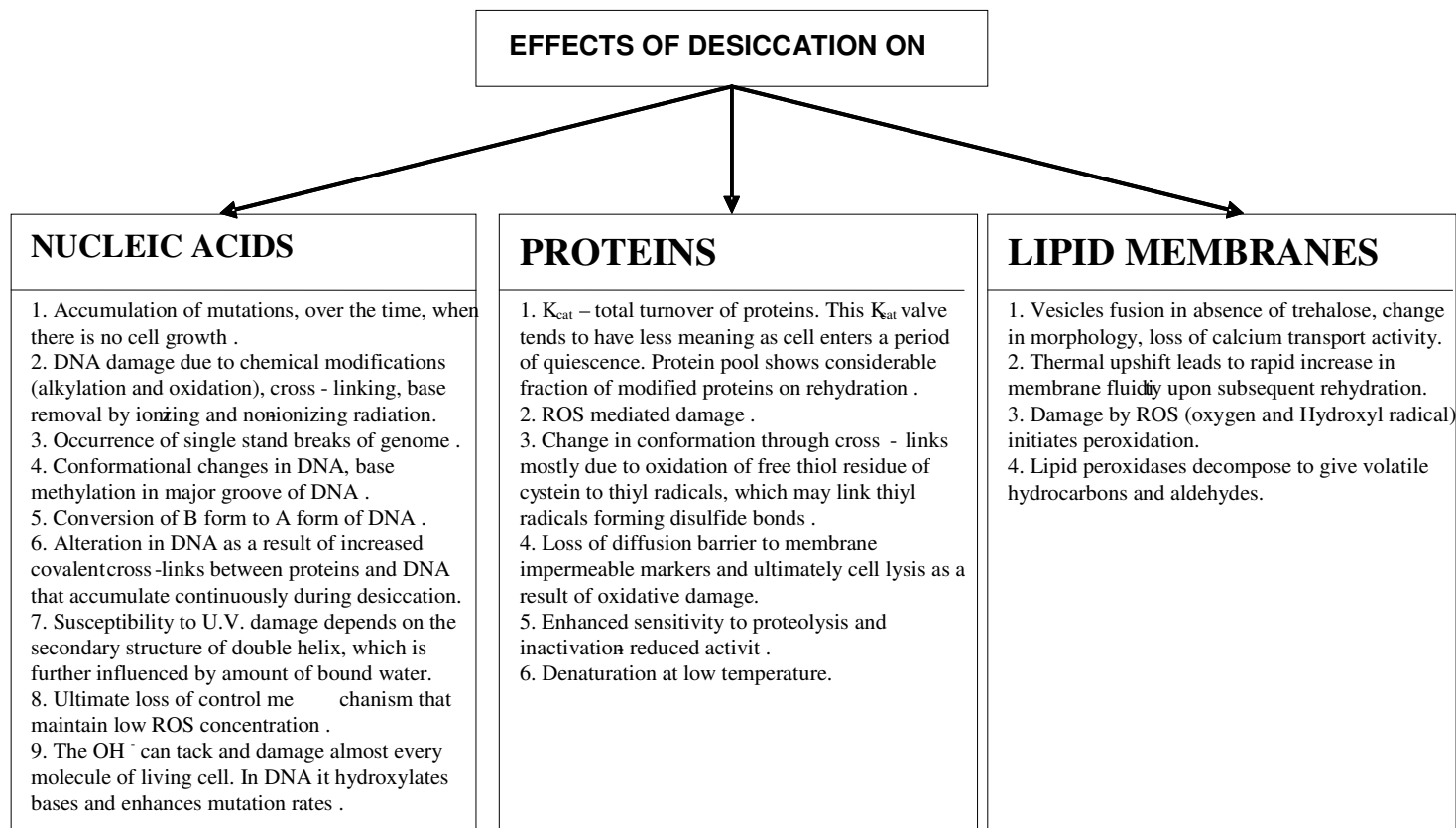


Figure 1. Highlights effect of desiccation on various biomolecules and its mechanism of tolerance in cyanobacteria.

(Jagar and Potts, 1998b). Multiple genome copies in cyanobacteria (Simon, 1980) are another mechanism of tolerance against DNA damage. Role of Histones-like DNA binding proteins such as HNS, HU, INF in association with topoisomerase, imparts regulation on DNA repair and nucleoid organization maintenance (Palchaudhari et al., 1998). Changes to one or more histones-like proteins to chromosomal DNA have potential to alter nucleoid organization and hence DNA topology (Palchaudhari et al., 1998). H-NS (136 amino acids) neutral protein function as homodimer in DNA. In addition to its role of nucleoid organization maintenance, H-NS also regulates transcription of many unlinked genes (Palchaudhari et al., 1998). Reduced water content influences photoproduct formation without causing conformational change in DNA (Lindsay and Murrell, 1983). Special "Repair Ligases" are also present that contribute a lot in DNA repair. Single strand breaks are repaired by these Ligases that are required for replication. The m-RNA isolated from *Nostoc commune* supported low rate of translation *in-vitro* in either homologous translation system, suggesting that they may be modified (Jagar and Potts, 1998b). Trehalose protects nucleic acids from desiccation because of accumulation in membranes (Potts, 2005).

Proteins

Bound water plays crucial role in protein folding and structure, which imparts stability to it during desiccation. Ubiquitin, which plays a role regulating lysis and selective degradation of proteins in eukaryotic cells, was identified and characterized in desiccated tolerant *Nostoc commune* UTEX 584 (Durner and Boger, 1995). The role of Ubiquitin in this cyanobacterium may be specific one because the unicellular form *Synechocystis* sp. PCC 6803 does not make the protein. Whether Ubiquitin playing a role in protein turn over during desiccation and rehydration of *Nostoc commune* UTEX 584 and other filamentous cyanobacteria remain to be determined. Water stress proteins (three 32; 37; 39) are secreted and accumulate in extracellular glycan sheath and show homologies with carbohydrate-modifying enzymes (Hill et al., 1994a). The Water stress proteins (Wsp) are immunologically related, the amino acid sequence at their termini is identical, they all appear to lack methionine residue. Water stress proteins have a structural role in cell stability in view of their abundance and their high content of hydroxylated amino acids (serine, threonine and tyrosine). Wsp polypeptides, and UV-absorbing pigments, form complexes in the absence of salt, exist in

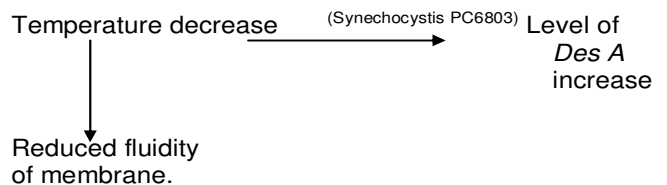
a monomeric state in the presence of salt (Hill et al., 1994a). Ionic interactions attenuated *in situ* through drying and wetting of colonies and the resultant changes in salt concentration (Potts, 1999). In the presence of salts, Wsp polypeptides appear to exist as monomers, while in the absence; Wsp undergoes apparent increase in molecular mass. Rehydration causes Wsp to show weak but pronounced Xylanase activity. A single polyphosphate granule, deposit within the nucleoplasm during rehydration. During desiccation cells accumulate massive amount of singular polypeptide, cyanophycin, which quickly disappears after rehydration (Peat et al., 1988). Cyanophycin found only in cyanobacteria. It is not synthesized on ribosomes, and contains only arginine and aspartic acid, in a 1:1 molar ratio (multi-l-arginyl-poly-l-aspartate, Allen, 1984). The arginine and aspartic acid used for cyanophycin synthesis presumably derive from rapid protein turnover upon rewetting of the cells because the onset of nitrogen fixation requires more extended periods of rehydration (Potts and Bowman, 1985; Rodgers, 1977; Scherer, 1991). Arginine HCl is a non-compatible solute and interact with the denatured state through its guanidinium group and thus induce structure destabilization (Timasheff, 1993). It is possible that the scavenging of arginine by multi-l-arginyl-poly-l-aspartate synthase may contribute to some stabilization of proteins. Catalase is another enzyme for damage repair (Gilichinsky et al., 1992) (Figure 6).

It has been suggested that sulphahydral may play a part in stabilization of desiccated cyanobacteria. Trehalose protects protein damage during desiccation by accumulation. Major response to high temperature is trigger to HS proteins formation. They are activated by accumulation of denatured proteins in cytoplasm. Dna K acts as temperature sensor. Dna K play critical role in regulation of the heat shock and negatively affect σ_{32} translation stability (Ibloya et al., 1997) and activity (Jhon McCarty and Graham Walker, 1991). Rpo H mutation causes the phenotypes to suppress; results into reduced σ_{32} activity. Dna K has a weak ATPase activity and function as molecular chaperone, it instigate λ and P1 replication and reactive heat denatured RNA polymerase in a manner dependent on ATP hydrolysis. Dna K autophosphorylated in presence of ATP and this is triggered by Ca^{++} ions. Ribosomes sensor hypothesis implies that the signal, which transduces the sensing of the temperature stress, to the increased expression of stress genes, is regulated by the level of translational process (Ruth et al., 1990). Depletion of 4.5s RNA alters translational capacity of cell compounds like alkanols; alter membrane fluidity and threshold temperature of the HS proteins. *Synechocystis* cell, when subjected to stress, four class of proteins (70, 60, 17 and 14 kDa) were induced. 17 kDa corresponds to Dna K (Jhon McCarty and Graham Walker, 1991), HSP60 encodes *gro ESL* operon and *cpn60* gen. HSP 14 was identified as *gro ES* (Figure 2).

Lipid membranes

Trehalose can stabilize membranes lipid layer (Crowe et al., 1986; 1992a, b; Leslie et al., 1994). Under desiccated conditions cell accumulates either one or both disaccharides— trehalose and sucrose (Potts, 1994). Trehalose replaces shell of water around macromolecules circumventing damaging effect during drying. Trehalose and sucrose behave as bacterial glass. They replace bound water and can form aqueous glasses around desiccated cells. Trehalose acts as substrate for trehalase enzyme, which is responsible for tolerance mechanism (Lee et al., 1989) (Figure 7). Water replacement hypothesis (Oliver et al., 1998) depresses gel to liquid crystallization phase temperature T_m upon rehydration. They expand phospholipid monolayer films (Lee et al., 1989). Membranes act as temperature sensor in cyanobacterial cells exposed to heat stress. Instead of thylakoid it is the plasma membrane, where putative primary heat stress signals are generated. Decrease in degree of unsaturation of fatty acids is the plasma membrane of cyanobacteria *Synechocystis* sp. PCC6803; enhance expression of *Des A* gene for $\Delta 12$ acyl-lipid desaturases on the shocking trigger of low temperature.

Lipid membrane acts as temperature preceptor of low temperature stress. The enzymes responsible for changing fluidity during temperature decrease are the “desaturases”, activity of which enhances at low temperature (Murata et al., 2000). Desaturases are responsible for introducing specific double bond into fatty acids of lipid. *Des A* gene encodes acyl-lipid desaturases that act at $\Delta 12$ position of fatty acid and is responsible for developing temperature compensation pathway.



Temperature induces changes (both high as well as low) in membrane fluidity is mediated by a membrane bound Histidine Kinase (Kaneko et al., 1995, 1996). The product of putative U3 genes for histidine kinase in genome of *Synechocystis* might be expected to function as sensor or transducer of environmental or intracellular stimuli (Suzuki et al., 2000). Say as *Hik 33* may span the membrane twice and forms a dimer, controlled by the temperature and the extent of unsaturation and fatty acids. When temperature is decreased or fatty acids are more saturated, the histidine kinase (residue in histidine kinase) domain may be phosphorylated. A phosphate group is then transferred to *Hik 19* and finally to *Rer*, which then regulates the expression of *des B* gene. *Hik 19.33* regulate *crh* and *des B* gene (Suzuki et al., 2000).

Other genes regulate two-component system

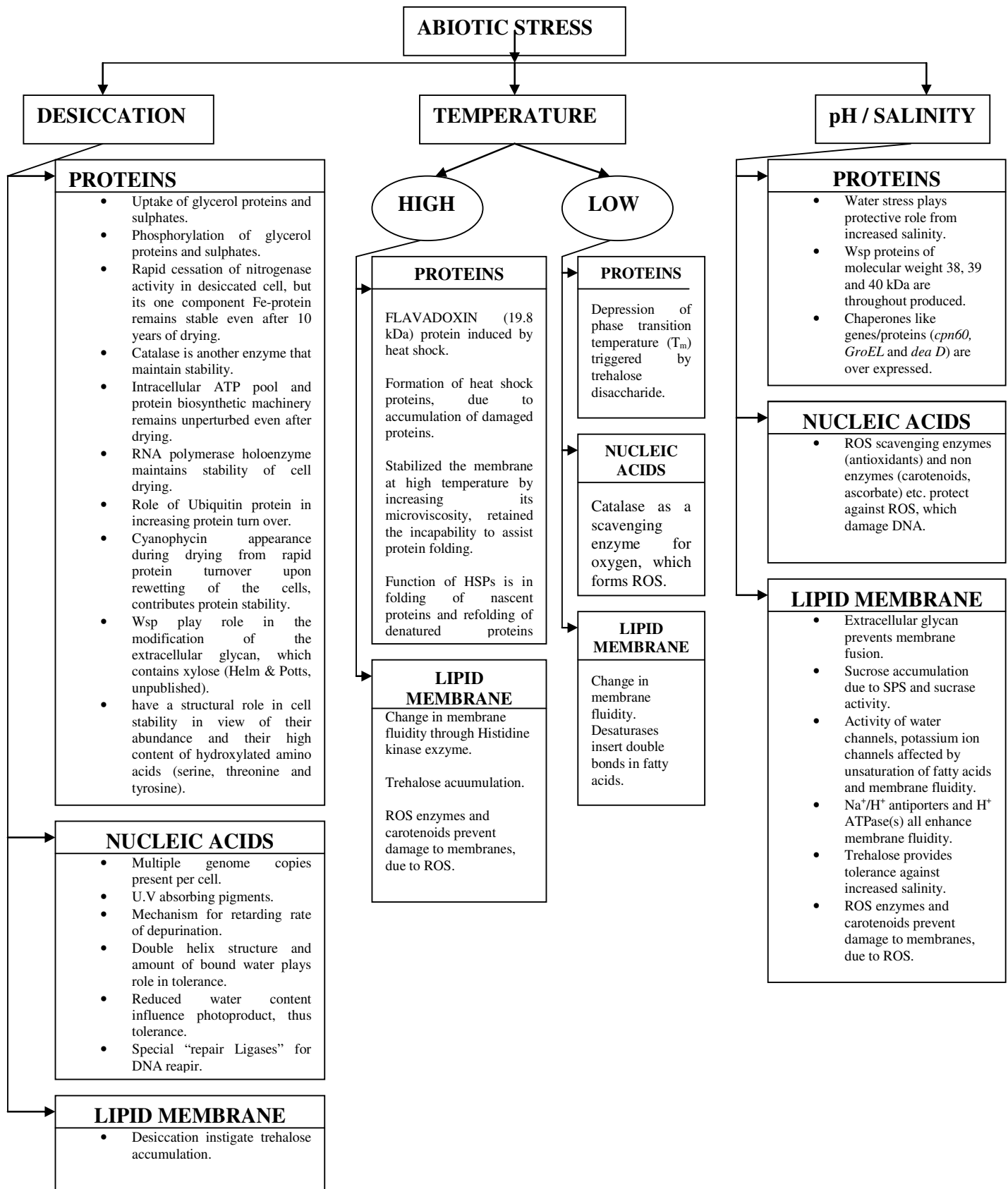


Figure 2. Shows various underlying stress tolerance mechanism in cyanobacteria which imparts growth and survival in various adverse conditions.

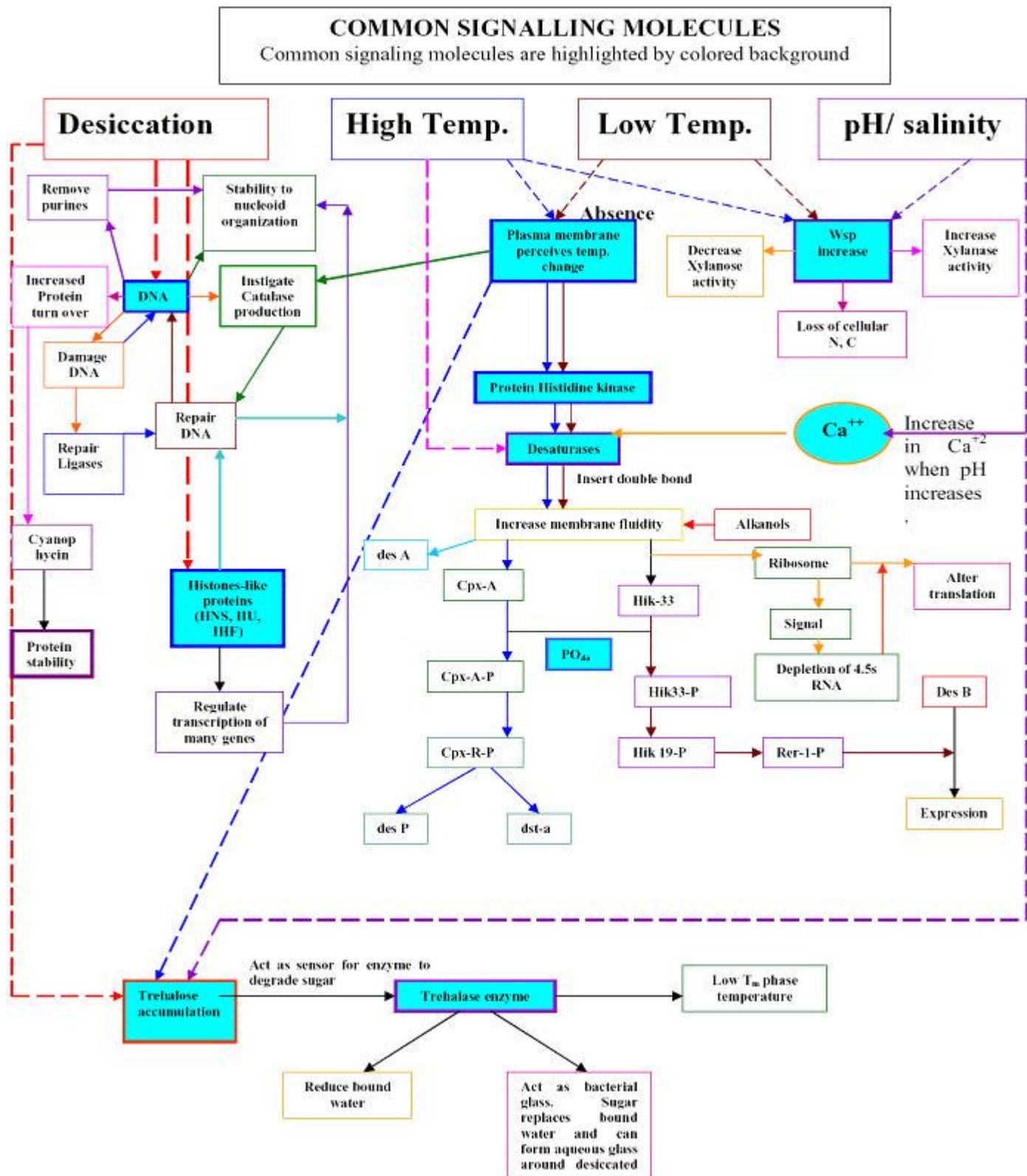


Figure 3. Common signaling molecules in various molecular pathways operating during stress conditions. Red line represents signaling operated due to desiccation Blue line represents stress signaling due to High temperature stress while brown line represents low temperature stress signaling. Purple line represents signaling concerned with pH/ Salinity stress. All highlighted and Dark filled boxes represents common signaling molecules which plays crucial role for combating abiotic or desiccation at nucleic acid, proteins or lipid membrane levels.

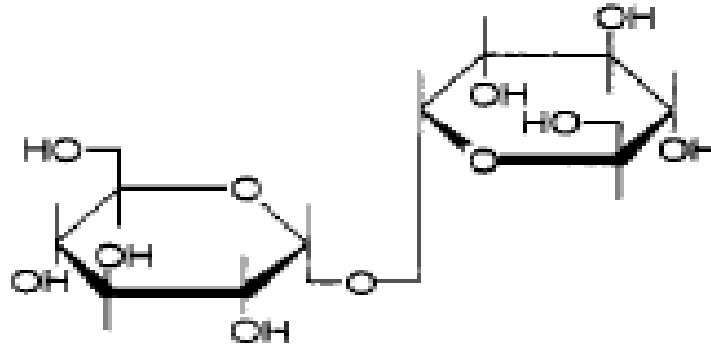


Figure 7. Molecular structure of trehalose. Source: Lee et al. (1989).

CPX-A – CPX-R. CPX-A is a histidine kinase, bound to plasma membrane and is autophosphorylated under high temperature stress. Phosphorylated CPX-A transfers a phosphate group to response regulator CPX-R which in turn activates transcription of several heat inducible genes such as *deg P* that encodes protease, *dsb A* encodes disulfide isomerase (Mileykovaskaya and Dowhan, 1997). Ca^{++} dependent protein phosphorylation might constitute a signal transduction pathway in triggering cold dependent gene expression (Monroy et al., 1993). The role of putative Na^+/H^+ antiporters encoded by *nha S1* (*slr 1727*), *nha S3* (*slr 0689*), *nha S4* (*slr 1595*), and *nha S5* (*slr0415*) in salt stress response and internal pH regulation of *Synechocystis* PCC6803. A Na^+/H^+ antiporter encode *nha S3* that is essential for cell viability. Salt adaptation includes two processes: (1) Synthesis and accumulation of compatible solutes. (2) Maintenance of low internal concentration of sodium ion by use of active export mechanism (Elanskaya et al., 2001). At high concentration of salt cyanobacteria actively extrude sodium ion and accumulate potassium ion and maintain internal ionic concentration. The transporter of these ions uses $\Delta\mu H^+$ by primary H^+ pump like H^+ -ATPase activity or respiratory cytochrome oxidase. Sodium cycle includes Na^+/H^+ antiporters, which maintain pH homeostasis in cyanobacteria at high pH, encoded by five genes *slr 1727=Nha S1*; *S110273=Nha S2*; *S110689=Nha S3*; *slr 1595=Nha S4*; and *slr 0415=Nha S5*. *Nha S2* is essential for uptake of Na^+ ion at low external concentration. Strains with low tolerance (up to 0.7 M NaCl) accumulate disaccharides sucrose and trehalose, strains with moderate tolerance (up to 1.8 M NaCl) accumulate heteroside GG (20-(α -D-Glucopyronosyl)-Glycerol) and strains with high salt concentration (up to 2.7 M NaCl) accumulate amino acid derivative Bet or Glutamatebetadine (Figure 3).

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