Stress response in cyanobacteria

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Abstract

Cyanobacteria are an important source of natural products. In this article, we briefly review the responses of cyanobacteria to different stresses. Abiotic stresses (temperature, salt, heavy metals, metalloid and ultraviolet (UV) influence cell growth and metabolism in cyanobacteria. Salt stress is a major abiotic factor that decreases the growth of cyanobacteria and affects the different processes including photosynthesis, respiration, and metabolism. The basic mechanisms for salinity adaptation include the active extrusion of inorganic ions and the accumulation of compatible solutes such as sucrose, trehalose, glucosyl glycerol, and glycine betaine. Cyanobacteria have a complex antioxidative system including enzymatic and nonenzymatic antioxidants for mitigation of oxidative damage under salt stress. Cyanobacteria have some defense mechanisms for the decline of the direct and indirect destructive effects of UV. These mechanisms include avoidance, scavenging of reactive oxygen species (ROS), synthesis of UV-absorbing/screening compounds such as mycosporine-like amino acids and scytonemin, repair of UV-induced damage in DNA, and resynthesis of proteins. Metals are involved in key metabolic pathways as redox cofactors in proteins. High concentration of metals causes the generation of ROS and oxidative damage. Thus, the major role of metal homeostasis in maintaining the intracellular concentration of metal within a range compatible with cell viability becomes evident. The biosynthesis of metabolites can be triggered by a number of abiotic stresses because they affect metabolic pathways.

Keywords: cyanobacteria; stress; tolerance; antioxidants; mitigation strategies; reactive oxygen species

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Introduction

Cyanobacteria are the first photosynthetic organisms that arose 3.5 billion years ago. Cyanobacteria are present in different environments including terrestrial, freshwater, and marine habitats, ice shelves, bare rocks, hot springs, and arctic and antarctic lakes (Fischer, 2008; Los and Murata, 1999; Stanier and Cohen-Bazire, 1977). Cyanobacteria are the major producers of biomass in aquatic environments and contain main compounds with agricultural, medicinal and industrial values (Cardozo et al., 2007; Singh et al., 2010; Whitton and Potts, 2000).

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Cyanobacteria add as natural biofertilizer for the fertility of the rice paddy fields due to their ability in nitrogen stabilization (Vaishampayan et al., 2001).

Cyanobacteria can survive in different environments (Rastogi and Sinha, 2009). Abiotic stresses lead to harmful effects in cells. Abiotic stresses include temperature, salt, heavy metals, metalloid, and ultraviolet (UV) influence on physiological and biochemical parameters in organisms. Extreme stresses can lead to the death of organisms. Cyanobacteria are used as models for the determination of defense strategies against stresses (Borowitzka, 2018; E. Beck et al., 2017). Cyanobacteria acclimate to various stresses by a change in physiological, biochemical, and molecular activities (Singh and Montgomery, 2011). This review provides an overview of the effects of different stresses on cyanobacteria and the defense mechanisms these prokaryotes have developed to cope with harmful effects of the stress.

Temperature stress

Cyanobacteria exist in all environments from antarctica, where the temperature never exceeds -20 °C, too hot springs, where the temperature reaches 70 °C (Psenner and Sattler, 1998; Ward et al., 1998). Temperature stress is an obvious stress that is caused by seasonally and daily changes. Cyanobacteria based on temperature tolerance are divided into four groups, namely psychrophilic, psychrotrophic, mesophilic, and thermophilic, with different optimum growth temperature. Psychrotrophics tolerate cold temperatures (below 15 °C); mesophilics can tolerate temperatures up to 50 °C and thermophilics can tolerate above 80 °C (Chintalapati et al., 2006; Meeks and Castenholz, 1971; Murata and Wada, 1995; Schuliger et al., 1993; Tasaka et al., 1996).

Changes in the components and metabolism of the cells depend on the duration and intensity of the temperature (Sung et al., 2003). Membranes include saturated and unsaturated fatty acids and changes in these fatty acids cause modification in membrane fluidity (Mansilla et al., 2004). One of the responses to temperature stress is the change in membrane composition, which involves alteration in membrane fluidity, saturation of fatty acids, and integrity of the proteins. Under high temperatures, changes that occur include excessive fluidity of the membrane, alteration in bonds between the polar groups of proteins, and ion leakage. In contrast, membranes have less fluidity at low temperatures (Morgan-Kiss et al., 2006; Singh et al., 2002). Reduction of temperature decreases the function of various enzymes and thus reduces the physiological and biochemical performance. The creation of ice crystals under low temperature causes membrane disruption and halting the chemical solution (Schuliger et al., 1993). Cyanobacteria have two protective mechanisms against cold stress. These mechanisms include the desaturation of membrane fatty acids and induction of enzymes that increase the efficiency of transcription and translation (Morgan-Kiss et al., 2006; Murata and Los, 1997; Sato, 1995).

Cyanobacteria regulate membrane fluidity under cold stress by alternation in fatty acids such as a decline in the content of C18:1(9) and C18:2(9,12) and enhancement in levels of C18:3(9,12,15). Acyl-lipid desaturases include Desa, DesB, DesC, and DesD in cyanobacteria by creation of a double bond in the Δ12, Δ15, Δ9, and Δ6 position cause unsaturation of fatty acids (Murata and Wada, 1992; Nishida and Murata, 1996). Sinetova and Los (2016) showed that more than 100 genes induced by cold stress. These genes are divided into six groups based on performance (signal perception and transduction, transcription and translation, cell wall and membrane maintenance, photosynthesis and respiration, various cellular functions (cofactor biosynthesis, nucleotide metabolism) and unknown functions). Cyanobacteria acclimate to low temperatures by a change in their transcription and translation machines and membranes. High temperatures cause denaturation of protein and DNA and increase membrane fluidity. Heat shock proteins (HSPs) subsequently function as chaperonins and associated proteases that assist protein refolding and cause high-temperature tolerance (Fig. I) (Inoue et al., 2001; Slabas et al., 2006; Schuliger et al., 1993).

Salt stress

High concentration of salt leads to an imbalance in water and ion homeostasis and osmotic and ionic stress as primary stress and oxidative stress as secondary stress. Osmotic stress is a physical stress and happens when the concentration of ions inside and outside the cell is different. Salinity affects cellular water potential, causes loss of water, and increases ion content (Na^+ and Cl^-) in the cell (Roberts 2005; Tijen and Ismail 2006; Zhu 2001). Two crucial problems occur in the presence of high salt concentration: water availability is lowered and the concentration of ions is increased. The high concentration of inorganic ions can have detrimental effects on cellular growth and metabolism. Cyanobacteria have various strategies including reduction in sodium uptake and its active efflux via Na^+/H^+ antiport, induction of organic compounds to protect the osmoticum, increased antioxidative defense system to detoxify the reactive oxygen species (ROS), and expressing a set of salt-inducible proteins to tolerate salt stress (Fig. II) (Ladas and Papageorigou, 2000; Tijen and Ismail, 2006).

Salt stress-induced oxidative stress and antioxidative defense system

Salt stress causes oxidative stress through an increase in ROS production such as superoxide, hydrogen peroxide, and hydroxyl radicals. These ROS are highly reactive and cause oxidative damage to lipids, proteins, and nucleic acids and change cellular metabolism. ROS, at low concentrations, play important roles in the cell such as lignification of cell wall, defense against pathogens, sensing, and adaptation to stress conditions and induction of apoptosis by modulation in gene expression; on the other hand, high concentration of various ROS causes oxidative burst (Imlay, 2003; Neill et al., 2002). Salinity increases ROS production by alternation in photosynthetic electron current, reduction in carbon assimilation and PS II activity (Foyer et al., 1994). Lipids play an important role in tolerance to various stresses in cyanobacteria. Lipids in thylakoid contain a high percentage of polyunsaturated fatty acids that are sensitive to

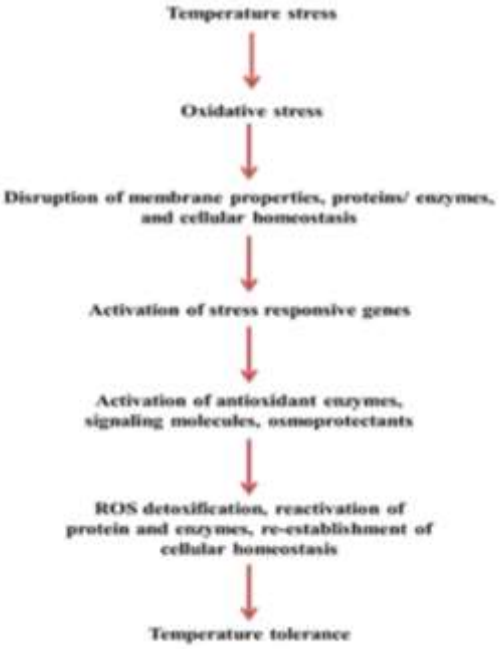

Fig. I. Schematic representation of the responses of a cyanobacteria cell to changes in temperature conditions (Dadheech, 2010).

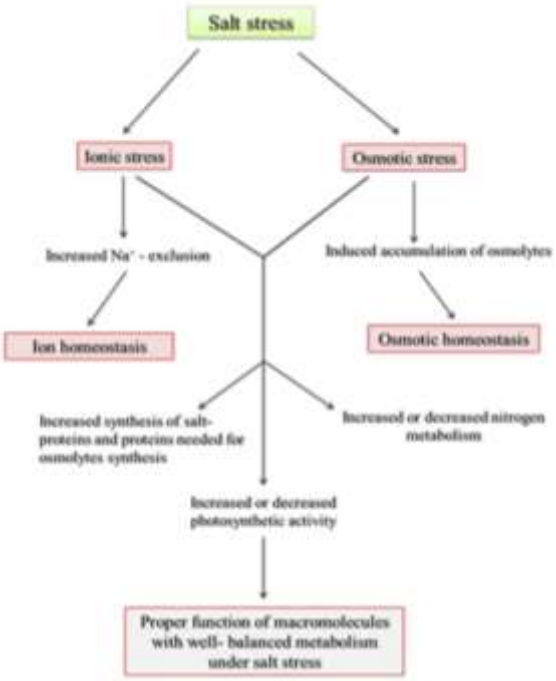

Fig. II. Physiological and biochemical changes in cyanobacteria under salt stress (Horie et al., 2012).

peroxidation. Salinity changes desaturation of fatty acids and fluidity of membrane, increasing malondialdehyde (MDA) content as a product of lipid peroxidation, and this parameter is an identifier for oxidative stress (Asish and Anath, 2005; Halliwell and Gutteridge, 1999; Meloni et

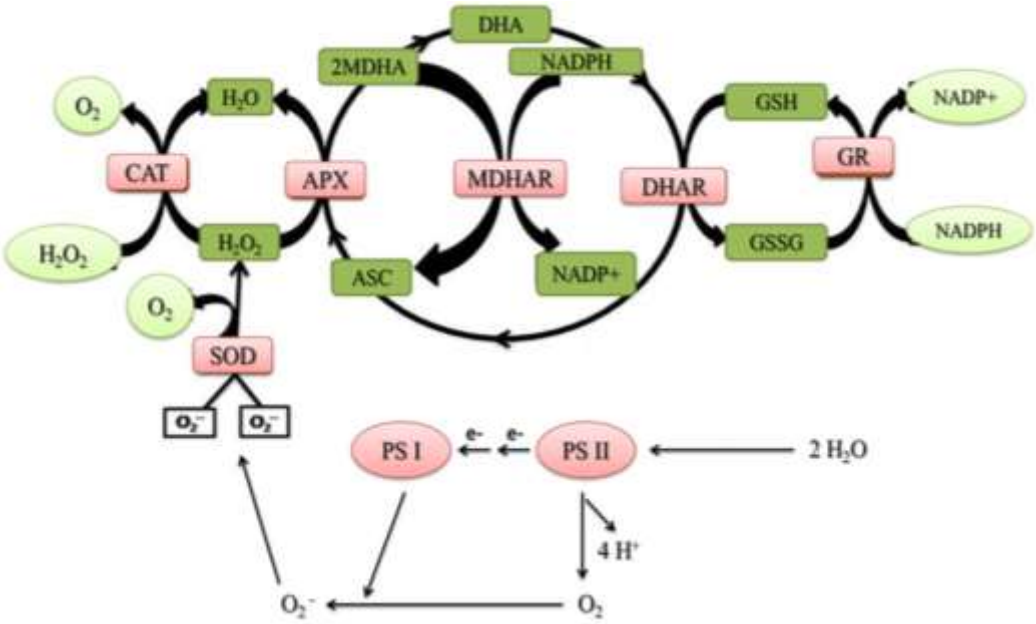

Fig. III. Schematic diagram showing the role of enzymatic and non-enzymatic antioxidative in ROS detoxification during salinity stress; ASC, Ascorbate; APX, Ascorbate peroxidase; CAT, Catalase; DHA, Dehydroascorbate; GSH, Glutathione; GR, Glutathione reductase; GSSG, glutathione disulfide; MDHA, Monodehydroascorbate; MDHAR, NAD(P)H-dependentoxido-reductase; SOD, Superoxide dismutase (Saha et al., 2015).

al., 2003; Singh et al., 2002). Cyanobacteria have developed a complex antioxidative system, including enzymatic system, consisting of superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione reductase (GR) and also non-enzymatic system consisting of carotenoid (CAR), ascorbate (ASA), glutathione (GSH), and α-tocopherol (α-TOC) for ameliorating ROS-induced oxidative stress (Fig. III) (Noctor and Foyer, 1998; Srivastava et al., 2005). SOD is the first enzyme in defense line that dismutates the O2-1 into H2O2 and has four isozymes depending on the metal cofactor (FeSOD, MnSOD, Cu/ZnSOD, and NiSOD) (McKersie and Leshem, 1994). NiSOD is only SOD in primitive cyanobacteria, Fe, and Mn found in the higher orders of cyanobacteria and Cu/ZnSOD is rare in cyanobacteria (Priya et al., 2007). Three types of SOD indicated in cyanobacteria, namely, Tolypothrix, Anabaena, and Lyngbya which are Mn-SOD, Fe-SOD, and Hy-SOD (Fe-Mn-SOD), respectively (Feierabend and Engel, 1986). Catalase has three groups including typical monofunctional catalases, bifunctional catalase peroxidases, and binuclear manganese catalases (Mn-catalases) (Zamocky et al., 2008). β-carotene is a non-enzymatic antioxidant that maintains the light harvesting pigments against photochemical damage. Tocopherol is a strong scavenger of H_2O_2 and OH^{-1} radicals and inhibits lipid peroxidation. ASA causes detoxification of a wide range of ROS, e.g., superoxide anion, singlet oxygen, and peroxide. GSH maintains the redox state and is a precursor for the biosynthesis of proline (Kim et al., 2005; Munne-Bosch and Alegre, 2000).

Compatible solutes accumulation under salt stress

Osmotic regulation is an important mechanism for stress tolerance in cyanobacteria. Compatible solutes have low molecular masses and lack net charge. The main function of compatible solutes is to increase internal osmolality, prevent water loss and plasmolysis, and therefore maintain osmoticum of the cell. These compounds also can directly protect enzymes and membranes against denaturation under salt stress (Borges et al., 2002; Bremer and Kramer, 2000). Sucrose, trehalose, glucosyl glycerol (GG), glutamate, and glycine betaine are common osmoprotectants in cyanobacteria. There is no universal compatible solute in all

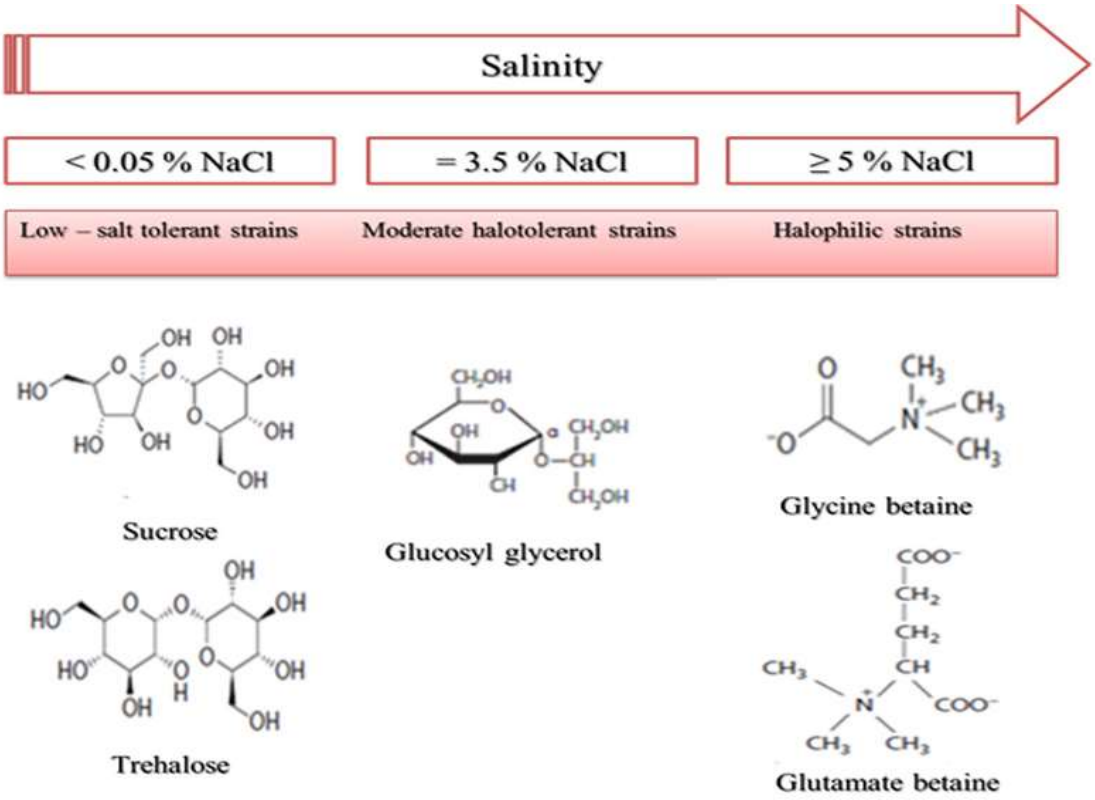

Fig. IV. Structure of major compatible solutes of cyanobacteria in correlation with their overall salt resistance (Hagemann,2011).

cyanobacteria. GG, glycine/glutamate betaine and sucrose are major solutes in Synechocystis PCC 6803, Spirulina and Nostocmuscorum, respectively (Reed et al., 1986; Marin et al., 2006). The type of compatible solute that accumulates in the cell depends on the degree of salt tolerance in cyanobacteria (Fig. IV). Low-salt tolerant strains (maximum tolerance up to 0.7 M NaCl) accumulate trehalose and/or sucrose; moderate halotolerant strains (maximum tolerance up to 1.25 M NaCl) accumulate glucosyl glycerol and glucosyl glycerate. Halophilic cyanobacteria tolerate a very high concentration of salt (maximum tolerance up to 2.5–3.5 M NaCl) and accumulate glycine betaine and glutamate betaine (Hagemann, 2011; Reed and Stewart, 1988). Cyanobacteria have biosynthetic pathways and uptake systems for the accumulation of compatible solutes under salt stress (Kempf and Bremer, 1998). Trehalose is a non-reducing disaccharide including two glucose molecules with a 1α–1α bond and is synthesized by trehalose phosphate synthase (TPS) and trehalose phosphate phosphatase (TPP). In the synthesis pathway of trehalose, glucose-6-phosphate accepts one glucose molecule by UDP-glucose to form trehalose-6-phosphate, which is catalyzed by TPS. Trehalose-6-phosphate is dephosphorylated by TPP to produce trehalose (Avonce et al., 2006). Trehalose causes the protection of membranes and proteins in cells under stress (Weisburd, 1988). Glycine betaine is createed by choline oxidation and glycine methylation that is the main osmoprotectant to maintain cyanobacteria under a high concentration of salt. Glucosyl glycerol phosphate synthase (GGPS) and glucosyl glycerol phosphate phosphatase (GGPP) are enzymes of glucosyl glycerol biosynthesis. Stability of cell division is the main function of glucosyl glycerol under salt stress. (Ferjani et al., 2003).

Effect of salt stress on photosynthesis, respiration, and metabolism

Salt stress affects cell processes including photosynthesis and respiration. Cyanobacteria have four multi-protein complexes including photosystem I (PSI), photosystem II (PS II),

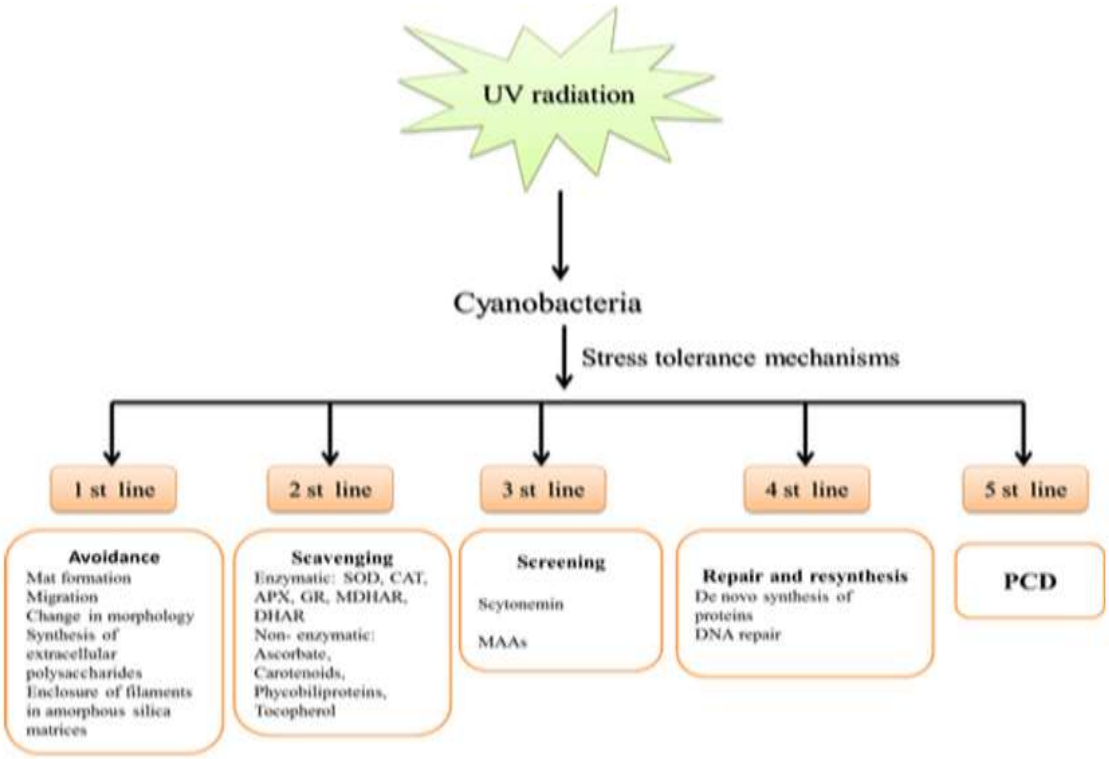

Fig. V. Schematic diagram showing the mitigation strategies employed by cyanobacteria to cope with UV (Singh et al., 2010).

cytochrome b/f complex, and ATP synthase, which is responsible for photosynthetic electron transport. Salt stress through the downregulation of PS II synthesis or upregulation of PS I reaction center increases the PSI activity and the PSI/PS II ratio. Salt stress by increasing the activity of ATP synthase provides the energy needed to enhance the active efflux of Na^+ and the protection of cellular homeostasis. Chlorophyll content changes based on the nature, habitat, and morphology of cyanobacteria. For instance, salt stress reduced chlorophyll content in Anabaena doliolum but induced it in Spirulina platensis (Lu and Vonshak, 1999; Srivastava et al., 2005). Another important pigment in cyanobacteria is phycobilin, which normally is associated with proteins to form phycobiliproteins. Salt stress reduced phycocyanin content in Spirulina platensis (Lu and Vonshak, 2002).

Salt stress influences dark reactions of photosynthesis. It reduces carbon assimilation and uptake of C14. Under conditions of carbon limitation as salinity, the oxygenase activity of Rubisco overcomes carboxylase activity (Moisander et al., 2002; Srivastava et al., 2008).

The cytoplasmic and thylakoid membranes are the sites of respiration and electron transport chain in these two membranes depends on the growth conditions. Respiration activity may induce in either one or both sites by salt stress (van Thor et al., 2000). Sodium plays an important role in nitrogen metabolism and nitrogenase activity by the effect of Na^+ on the transport of cations such as Ca^{2+}, which is essential for heterocyst differentiation, and anions like phosphate, amino acid, and sugars (Allen and Arnon, 1955). Nitrogenase activity was reported to be induced under salt stress in Anabaena doliolum while it reduced in Nostocmuscorum (Bhargava and Singh, 2006; Rai et al., 2001).

Salt stress changes proteome and gene expression

Salt stress changes the metabolism of the cell through modification in proteins and gene expression. Proteins are one of the main goals of salinity and this stress through oxidative stress causes damage to proteins. ROS cause oxidation of cysteine (SH) to cysteine (S-S), methionine to methionine sulfoxide, and formation of 3,4-dihydroxyphenylalanine (DOPA) and various hydroxyleucines from tyrosine and leucine (Hagemann et al., 1999). Change in protein is the final line of salt tolerance (Duche et al., 2002). Salt stress causes three changes in protein profile including induction of a group of proteins, suppression of another group of proteins and expression of a new set of proteins that are salt-responsive proteins. The change in protein under salinity contains early shock response (displayed just after the onset of salt stress) and late adoptive response (shown when the organism is exposed to salt stress for a long time) (Apte and Bhagwat, 1989; Fulda et al., 2006). Two-component systems have important roles in the sensing different signals from the environment in cyanobacteria. These systems include a sensory histidine kinase (Hik) and a corresponding response regulator (Rre) protein that acts as a transcriptional activator/repressor (Los et al., 2010; Marin et al., 2003). Salt stress induced ribosomal protein genes (rpl2, rpl3, rpl4, and rpl23) for protection of ribosome activity, FtsH, a gene responsible for the degradation of photodamaged D1 protein, glpD and ggpS genes for proteins involved in the synthesis of GG to overcome the osmotic stress induced by salt stress and expression of heat shock proteins and chaperones (HSPA, dnaK, dnaJ, htrA, groEL2, and clpB) to inhibit accumulation of denatured proteins (Nissen et al., 2000).

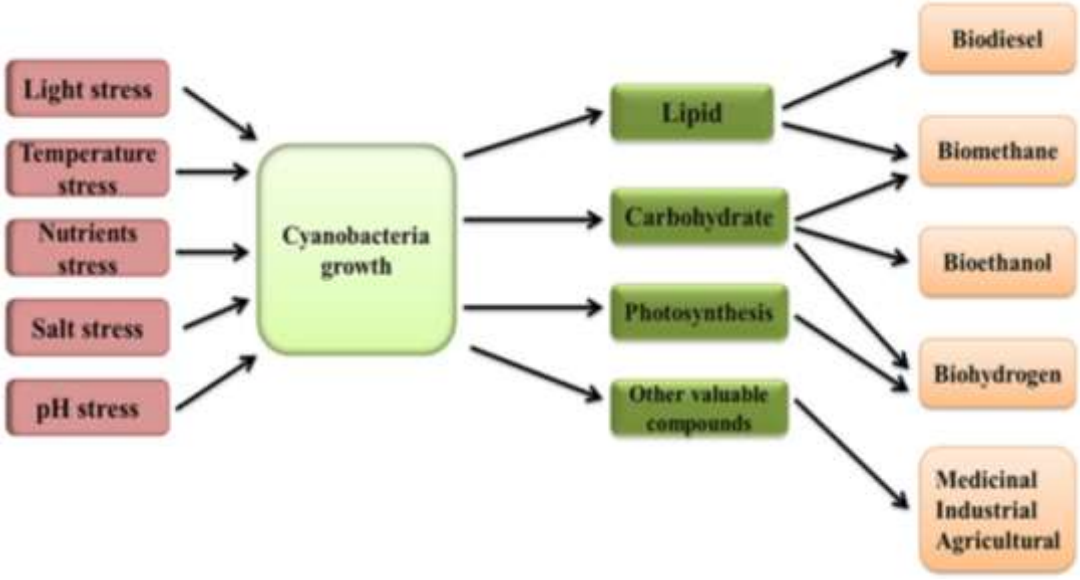

Fig. VI. A model for assessment of environmental stresses for enhanced biofuel production and other valuable compounds (Cheng and He, 2014).

UV stress

UV is the only radiation that causes stress. When the ozone layer is reduced, cyanobacteria are exposed to a high level of UV-B radiation (280-320 nm) (Singh et al., 2010). UV affects various cell processes including morphology, cell differentiation, survival, growth, N2 metabolism, pigmentation, motility and orientation, phycobiliprotein composition, protein profile, DNA and CO_2 uptake (Blakefield and Harris, 1994; Gao et al., 2007; Lesser, 2008; Sinha et al., 2008). UV radiation causes photo-bleaching of photosynthetic pigments; reduction in phycobiliproteins content, disassembling phycobilisome complex, decreasing other photosynthetic parameters such as 14CO2 uptake, O2 evolution and Rubisco activity in cyanobacteria (Sinha et al., 1995; Sinha et al., 2008). UV stress also induces the peroxidation of PUFA by oxidative burst which subsequently affects thylakoid membranes and the cellular integrity (He and Hader, 2002). UV-B stress increased MDA content

in Cylindrospermum sp. (Chris et al., 2006). UV-B decreased growth in Nostocmuscorum and Phormidiumfoveolarum (Singh et al., 2011).

Cyanobacteria have five mechanisms include avoidance, scavenging of ROS, synthesis of UV-screening/absorbing compounds such as scytonemin and mycosporine-like amino acids (MAAs), repairing UV-induced damage in DNA, and re-synthesizing proteins for dealing with the negative effects of UV stress (Fig. V).

Avoidance is the first line of defense in cyanobacteria against UV stress. This mechanism includes movement from high to low UV levels in the water column, change in morphology to increase self-shading, formation of mats containing different cyanobacteria species or filaments enclosed in amorphous silica matrices, and synthesis of extracellular polysaccharides. Moving cyanobacteria to mat areas and depth of water protects them from UV irradiance (Reynolds et al. 1987; Quesada and Vincent, 1997; Vaara, 1982).

UV by interacting with oxygen and other organic compounds causes oxidative damage to cells. An antioxidative system is the second line of defense in cyanobacteria that overcomes oxidative damage. This system includes enzymatic (CAT, SOD and glutathione peroxidase (GSH-Px)) and non-enzymatic antioxidants (ascorbate (vitamin C), a-tocopherol (vitamin E), carotenoids and reduced glutathione) (He and Hader, 2002; Niyogi, 1999). UV stress increased the activity of SOD and APX in Nostocspongiaeforme and Phormidium corium (Bhandari and Sharma, 2006).

Screening of damaging UVR by UV-absorbing compounds is the third line of defense under UV stress. MAAs and scytonemin are UV-absorbing/screening compounds that maintain the organism against UV radiation. MAAs are water-soluble compounds, small (<400 Da) and colorless that protect cells by elimination excess energy into the form of heat to their surroundings. They can also act as antioxidants to maintain against ROS under UV stress. Scytonemin is a yellow-brown lipid soluble and inducible pigment located in the extracellular polysaccharide sheath and is another UV-screening compound in cyanobacteria. (Bultel-Poncé et al., 2004; Coba et al., 2009; Cockell and Knowland, 1999; Sinha and Hader, 2008).

UV stress causes direct and indirect harm to DNA through the absorption of UV-B radiation and oxidative stress, respectively. Direct absorption of UV-B causes the production of dimeric photoproducts such as cis-syncyclobutane pyrimidine dimers (CPDs) and pyrimidine (6-4) pyrimidone photoproducts (6-4 PPs) in DNA. Oxidative stress causes single- or double-strand breaks in DNA molecule. The repair and resynthesis of sensitive targets is the fourth line of defense against UV stress. The mechanisms of DNA repair include photoreactivation by photolyase which converts formed dimers into monomers, excision, and recombination repair helps cope with UV stress (He and Hader, 2002; Rastogi and Sinha, 2011; Xie et al., 2009). Cyanobacteria use apoptosis or programmed cell death (PCD) when the cell is damaged after repair under UV stress (Ning et al., 2002). Hsps are a group of stress proteins that by the effect on DNA repair mechanisms or induction of apoptosis play an important role in tolerance to UV stress (Torok et al., 2001; Verschooten et al., 2006).

Metals and metalloid stress

Metal ions have many roles including those of manganese (Mn) in the oxygen-evolving photosynthetic complex; iron (Fe) in photosynthesis; magnesium (Mg) in chlorophyll, ATPases and kinases; Molybdenum (Mo) in sulfite oxidases, nitrogenases, and nitrate reductases; copper (Cu) in cytochrome oxidase and plastocyanin in cyanobacteria. In addition, cyanobacteria are involved in some heavy metals that do not have a nutritional role, including arsenic (As), cadmium (Cd), aluminum (Al), cesium (Cs), mercury (Hg) or lead (Pb). Cyanobacteria have mechanisms for supplying metals as much as they need (Blindauer, 2008; Tchounwou et al., 2012; Kranzler et al., 2013). Cyanobacteria protect metallic homeostasis through various mechanisms include alteration of membrane structure, activation or inactivation of the transfer pumps, biotransformation, and sequestering (Bruins et al., 2000; Hantke, 2005; Mire et al., 2004; Ybarra and Webb, 1999). High concentrations of zinc and copper produce ROS in cyanobacteria and they are applied from enzymatic and non-enzymatic antioxidants for ROS detoxification (Xu et al.,

2010). High level of copper can damage photosynthesis and cellular redox balance, and can change the ultrastructure of cell that usually leads to death (Nagalakshmi, 2001). Phosphorus deficiency causes the reduction of photophosphorylation; creates a highly excited state of thylakoid membranes, the decline in electron transport, and disruption in photosynthesis. Cyanobacteria can fight phosphorus deficiency by the production of extracellular phosphatases (Bhaya et al., 2000; Wang et al., 2010). Metallothioneins (MT) are small cysteine-rich proteins that are linked to metals (such as As, Cd, Cu, Hg, and Zn), and for the first time were identified in cyanobacteria that tolerate high concentration of Cd or Zn (Blindauer, 2011).

pH stress

PH affects various physiological and biochemical processes and growth in cyanobacteria. Cell function in cyanobacteria depends on to maintain the pH in a specific range. Cyanobacteria maintain inside and outside pH of the cell between 7.1-7.5 and 5-10, respectively. The change in pH causes alternation in cellular processes such as bioavailability of nutrients, transport of substances across cytoplasmic membranes, the activity of enzymes, photosynthetic electron transport, and osmotic potential of cytoplasm. Reduction in extracellular pH decreases intracellular pH, affects cellular wall biosynthesis and transfer of solutes, and increases maintenance of the needed energy and may reduce growth (Giraldez-Ruiz et al., 1997; Kallas and Castenholz, 1982; Stumn and Morgan, 1981; Walsby, 1982). Many mechanisms regulate pH homeostasis and CO_2/ HCO_3 concentration including expression of proteins involved in carbon assimilation and pH homeostasis, adjustments in carbonic anhydrase activity, and/or induction of acetolactate ions. Oxalate decarboxylase and carbonic anhydrase have a role in pH homeostasis that is induced under pH stress (Battchikova et al., 2010; Katoh et al., 2001).

Abiotic stresses as tools for metabolites in cyanobacteria

A number of cyanobacteria can produce valuable compounds such as chlorophyll, β-carotene, astaxanthin, xanthophylls, and phycobiliprotein. In addition, cyanobacteria such as Phormidium sp., Spirulina platensis, Lyngbya majuscule, and Schizochytrium sp. are a source of different compounds such as polysaccharides, lipids, proteins, vitamins, sterols and enzymes. Cyanobacteria are also a natural source of antioxidants because of bioactive compounds (Begum et al., 2016; Sorensen et al., 2013; Pulz and Gross, 2004). Full understanding of adaptation processes to stress in cyanobacteria has great value for the future biotechnological applications of cyanobacteria as a chemical feedstock and for the production of biofuels or high-value products. Cyanobacteria are a good source for the production of biofuels because of their rapid growth and photosynthesis potential (Wang et al., 2012). Cyanobacteria respond to environmental changes (abiotic stress factors) by alteration in their metabolites. Salt stress and nitrogen deficiency are stress conditions that are used to produce biodiesel (Paliwal et al., 2017). High light and salt stress increased total lipid content in Nannochloropsis sp. (Pal et al., 2011). Cyanobacteria are used as cell factories due to the production of compatible solutes in response to salinity. Recently, an efficient production system for sucrose was described using the cyanobacterium Synechococcus elongates PCC 7942 (Ducat et al., 2012). The lipids in cyanobacteria are mainly in the form of esters of glycerol and fatty acids, which are suitable for biodiesel production. A number of factors are known to influence the lipid content of cyanobacteria, such as nitrogen and silicon deficiency, phosphate limitation, and high salinity (Chisti, 2007; George et al., 2014; Illman et al., 2000; Lynn et al., 2000).

Conclusion

Cyanobacteria have several targets susceptible to abiotic stresses; however, these organisms have developed defense mechanisms that sustain their successful growth and survival under various stress conditions. Cyanobacteria respond to the changing environmental condition (abiotic stress factors) by modulation of their metabolites; therefore, stress conditions are

applied for the commercial production of feedstock for biodiesel production and other valuable compounds. Although information about the diverse aspects of stress effects has been accumulated in the last few decades, gaps remain that prevent a clear understanding of the stress tolerance mechanisms of cyanobacteria. Overall, it seems that their stress tolerance mechanisms have allowed cyanobacteria to become the most ecologically successful prokaryotes on Earth.

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