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Short Commentary Open Access

UV-Induced Oxidative Stress in Cyanobacteria: How Life is able to Survive?

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Short Communication

Cyanobacteria are the most primitive and important prokaryotic component of photoautotrophic microflora on the planet Earth. They are ubiquitous in nature [1], maintaining the trophic energy dynamics of aquatic and terrestrial ecosystems [2,3]. Probably, they appeared on the Earth between 2.8-3.5 billion years ago during the Precambrian era [4] and led to the evolution of existing aerobic life on the Earth's atmosphere due to their inherent capacity of photosynthesis mediated oxygen evolution [5]. Adaptive diversification and inclusive survival of cyanobacteria in a range of ecological niches has ensued a large and diverse array of photosynthetic and other biomolecules, each with specialized functions to compete them successfully on the planet. These organisms have inherent capacity to fix atmospheric nitrogen and are source of several natural products of high economic values [6]. They play an important role in the nutrient (e.g. nitrogen, carbon, and oxygen) cycles and are being employed as a potential source of biofuels or green energy.

During the past few decades, increase in solar ultraviolet (UV) radiation due to anthropogenically released ozone depleting substances has aroused severe concerns about its deleterious effects on all sun-exposed organisms including cyanobacteria [7,8]. Being an obligate photo-autotroph and crucial demand of photo-energy to maintain the normal cellular physiology and biochemistry exposes cyanobacteria to a wide range of fluctuating environments of intense solar radiation with high UV (280-400 nm) fluxes in their natural habitats. Herein, the recent advances on survival of cyanobacteria against UV-induced oxidative stress have been briefly discussed.

UV radiation (particularly UV-B: 280-315 nm) may lead to oxidative stress in cyanobacteria by upsetting the cellular redox status. In photosynthetic organisms including cyanobacteria, ROS are generated by means of photosynthetic electron transport chain [9]. In contrast to algae and higher plants, cyanobacteria undergo a high degree of O_2 reduction by consuming about 50 % of the photosynthetic electrons instead of only 15 % for plants [10]. It has been found that UV-B radiation has great efficacy to produce the reactive oxygen species (ROS) in cyanobacteria (Figure 1) [11].

Photo-induced oxidative stress may damage the cellular as well as biochemical integrity of a cell [12]. The high-energy short wavelength UV-B radiation may affect the biological systems either through direct effects on cellular DNA and proteins or indirectly by the generation of ROS [13,14]. It has been established that UV-A (315-400 nm) radiation which is not absorbed directly by the DNA molecules, can still damage it by producing a secondary DNA photoproducts via indirect photosensitizing reactions [15]. UV-B radiation brings about chemical modifications in DNA by the formation of purine/pyrimidine dimers (Figure 2) and strand breaks leading to mutagenesis and loss of normal cellular metabolic functions [16,17]. UV-induced oxidative stress may also induce DNA-DNA and DNA-protein cross links, base modifications and translocations [18]. It has been reported that DNA damage caused by UV radiation or ROS such as OH- radical results in ATM mediated phosphorylation of BID protein that induces cell-cycle arrest in S-phase [19,20]. Several oxidation products of purine bases such as 8-oxo-7,8-dihydroguanyl (8-oxoGua), 8-oxo-Ade, 6-diamino-4-hydroxy-5-formamidoguanine (FapyGua), FapyAde, and oxazolone have been reported to form upon exposure of DNA to UV-induced ROS [21-23]. UV-induced oxidative stress may damage proteins by site specific modifications of amino acid, aggregation of cross-linked reaction products, increased susceptibility to proteolysis and fragmentation of the peptide chain and oxidation of specific amino acids. ROS-mediated damage to photosynthetic apparatus followed by inhibition of photosynthesis has also been observed in cyanobacteria [16].

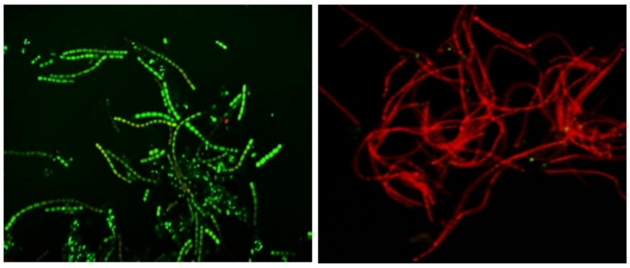

Figure 1: UV-induced generation of reactive oxygen species in the cyanobacterium Anabaena sp. A- UV-B exposed cells, B- UV-B control cells [11].

ROS are inevitably produced as intermediates of O_2 reduction, or by its energization. It has been shown that intense solar light beyond the normal capacity of the photosynthetic electron flow may cause production of other ROS along with $1O_2$ leading to inactivation of photosystems. Moreover, ROS are mainly produced by PSI; however, light-driven oxidation of water occurs in PS-II and under certain conditions, PSII contributes to the overall production of ROS in the thylakoid membrane of plants, algae and cyanobacteria [24]. It has been stated that $1O_2$ produced by an energy input to oxygen (O_2) from photosensitized chlorophyll, is believed to inhibit the repair of photosystem II (PSII). The singlet oxygen ($1O_2$), superoxide anion (O_2-), hydroxyl radical ($OH^{\cdot}$) and hydrogen peroxide (H_2O_2) are potent free radicals. The ROS $1O_2$ and $OH^{\cdot}$ produced by energy input to oxygen, is believed to be highly reactive, and reacts with important cellular molecules such as DNA, proteins, pigments, lipids and enzymes leading to cell death. ROS reacts with fatty acids in the membrane lipid bilayer, cause lipid peroxidation leading to membrane leakage. Moreover, the general mechanisms of ROS-induced damage

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of biomolecules or dysfunction of cellular activities have been well documented [9,25-27]. Overall, UV-induced oxidative stress may affect the cellular morphology and vital processes such as cell growth and differentiation, motility and orientation, pigmentation and photosynthesis, N_2/CO_2 metabolism, enzyme activity as well as alteration in the native structure of proteins and DNA of cyanobacteria (Figure 3) [7,28-31].

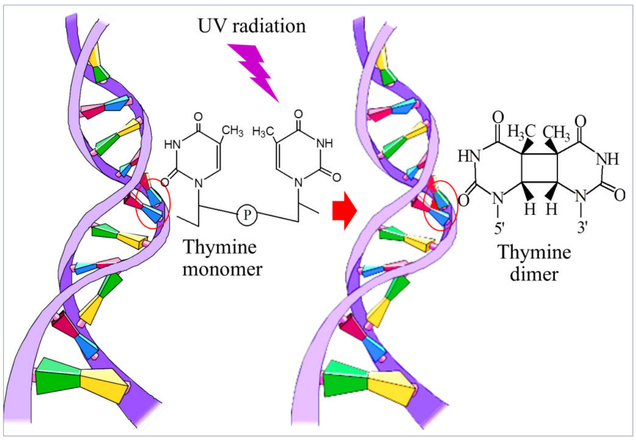

Figure 2: UV-B-induced formation of cyaclobutane thymine dimer on DNA strand.

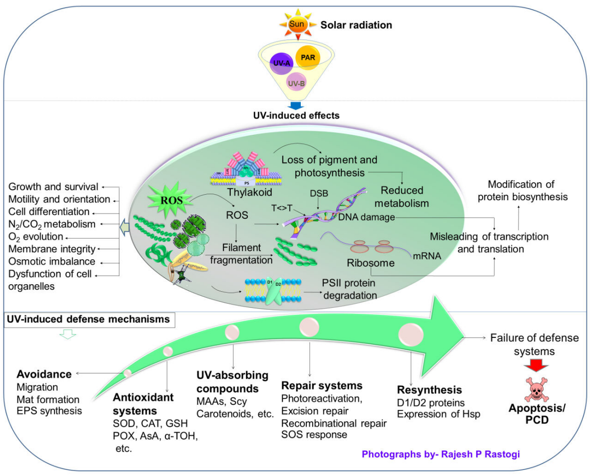

Figure 3: Effects of solar UV radiation on diverse photosynthetic life including cyanobacteria, and subsequent adoption of different defense mechanisms to counteract the harmful effects of short wavelength solar energy (modified from [7]).

Moreover, in-spite of several detrimental effects of UV-induced ROS and oxidative stress at cellular and biochemical levels as stated above, how cyanobacteria are still surviving and growing well in their natural habitats with high solar insolation? In fact, during the course of evolution cyanobacteria have developed several defence mechanisms such as avoidance (eg. migration and mat formation), DNA repair and heat dissipation mechanisms, synthesis of UV-absorbing/screening compounds and several antioxidant systems to counteract the damaging effects of UV-induced oxidative stress (Figure 3) [7,14,32].

A number of enzymatic (eg. ascorbate peroxidase, superoxide dismutase, catalase, glutathione peroxidase, glutathione reductase) and non-enzymatic (eg. carotenoids, ascorbic acid, α-tocopherols and reduced glutathione) antioxidant defence mechanisms operated in cyanobacteria to minimize the UV-induced oxidative damage caused by ROS. The presence of antioxidant systems may exclusively regulate the homeostasis of ROS formation in cells. Some other group of secondary compounds such as polyamines with free radical scavenging activity have also been reported in cyanobacteria [33].

Cyanobacteria are capable of protecting themselves from harmful solar UV radiation by synthesizing some UV-absorbing/screening secondary biomolecules, such as the mycosporine-like amino acids (MAAs) and scytonemin (Scy) [34-38]. MAAs are intracellular, small, colorless and water-soluble molecules consisting of cyclohexenone or cyclohexenimine chromophores conjugated with the nitrogen substituent of an amino acids or its imino alcohol. Strong UV absorption maxima, high molar extinction coefficients, UV inducibility, stability against different abiotic factors such as temperature and UV radiation and potential antioxidant function strongly favour the UV-photoprotective role of MAAs in cyanobacteria. MAAs have capability to dissipate absorbed radiation efficiently as heat without producing ROS [39]. Some of the common MAAs found in cyanobacteria have been represented in (Figure 4). Scy (λmax: 386 nm) is a yellow-brown lipid soluble pigment located in the extracellular polysaccharide sheath of some cyanobacteria (Figure 5) and protect them from UV radiation [40]. The synthesis of extracellular polysaccharides (EPS) also plays an important role in mitigation strategy against desiccation and harmful effects of UV radiation [41,42].

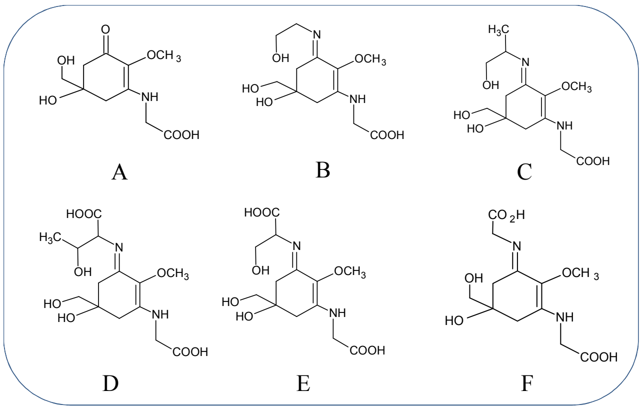

Figure 4: Chemical structure of some common MAAs reported in cyanobacteria. A-Mycosporine-glycine (λmax 310 nm), B-Asterina-330 (λmax 330 nm), C-Palythinol (λmax 332 nm), D-Porphyra-334 (λmax 334 nm), E- Shinorine (λmax 334 nm) and F-Mycosporine-2-glycine (λmax 334 nm).

Besides the role of UV-absorbing/screening compounds, the energy-dissipation mechanisms also play a vital role in photoprotection of cyanobacteria. It has been shown that under high light condition, the photoprotective heat/energy-dissipation mechanisms are activated that allow dissipation of excess energy in the form of heat by means of different pathway [9,43].

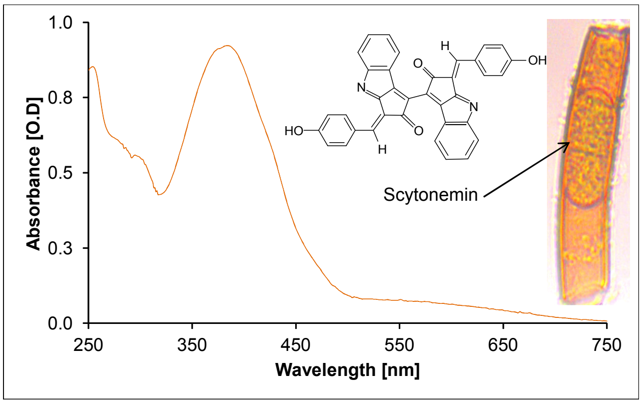

Figure 5: Extrcellular sheath pigment scytonemin and its UV-absorption maximum at 386 nm in the cyanobacterium *Lyngbya* sp.

It has been reported that most of the cyanobacteria can dissipate energy from phycobilisomes by means of photoactive soluble orange carotenoid protein (OCP) [43].

A number of repair mechanisms such as photoreactivation, excision repair such as base excision repair (BER) and nucleotide excision repair (NER) and recombinational repair have been reported in several organisms including cyanobacteria [14,44]. Photoreactivation (Figure 6) is the most efficient DNA repair mechanisms in cyanobacteria. The enzyme DNA photolyase play a vital role in photoreversal of the most cytotoxic and mutagenic DNA lesions such as cyclobutane thymine dimers (T<>T) or 6-4PPs. The enzyme photolyase binds precisely to the CPDs (for CPD photolyase) or 6-4PPs (for 6-4 photolyase) and directly monomerizes the cyclobutane ring of the purine/pyrimidine DNA lesion using the energy of visible/blue-light and protects the genome from damaging effects of UV radiation [45,46].

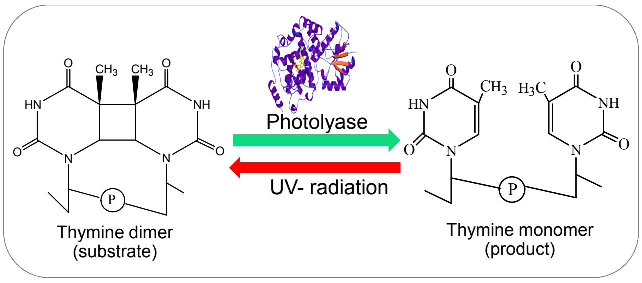

Figure 6: Photoreversal of thymine dimer in the presence of photolyase [14].

Overall, oxidative-stress-induced changes in general physiology and biochemistry may constitute ubiquitous threat to the accurate maintenance of the cellular and genomic integrity and survival of organisms; however, certain life forms such as cyanobacteria have motivated and devised a number of biochemical defence mechanisms to preserve their cellular machinery for competent endurance in adverse environment of UV-induced oxidative stress.

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