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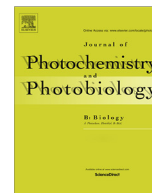

Short Review

Ultraviolet radiation and cyanobacteria

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ABSTRACT

Cyanobacteria are the dominant photosynthetic prokaryotes from an ecological, economical, or evolutionary perspective, and depend on solar energy to conduct their normal life processes. However, the marked increase in solar ultraviolet radiation (UVR) caused by the continuous depletion of the stratospheric ozone shield has fueled serious concerns about the ecological consequences for all living organisms, including cyanobacteria. UV-B radiation can damage cellular DNA and several physiological and biochemical processes in cyanobacterial cells, either directly, through its interaction with certain biomolecules that absorb in the UV range, or indirectly, with the oxidative stress exerted by reactive oxygen species. However, cyanobacteria have a long history of survival on Earth, and they predate the existence of the present ozone shield. To withstand the detrimental effects of solar UVR, these prokaryotes have evolved several lines of defense and various tolerance mechanisms, including avoidance, antioxidant production, DNA repair, protein resynthesis, programmed cell death, and the synthesis of UV-absorbing/screening compounds, such as mycosporine-like amino acids (MAAs) and scytonemin. This study critically reviews the current information on the effects of UVR on several physiological and biochemical processes of cyanobacteria and the various tolerance mechanisms they have developed. Genomic insights into the biosynthesis of MAAs and scytonemin and recent advances in our understanding of the roles of exopolysaccharides and heat shock proteins in photoprotection are also discussed.

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1. Introduction

Cyanobacteria, phylogenetically the most primitive group of Gram-negative bacteria, constitute a heterogeneous assemblage of photosynthetic oxygen-evolving prokaryotes that probably appeared on Earth during the Precambrian era (2.8–3.5 × 10^9 years ago) and created the oxygenic environment that supported the evolution of presently existing life forms. Cyanobacteria are ubiquitous in terrestrial, freshwater and marine habitats, but can survive in almost all habitats, including bare rocks, ice shelves, hot springs, and Arctic and Antarctic lakes, and also as endosymbionts in plants, lichens, protists and even animals.

Cyanobacteria are the major biomass producers globally, both in aquatic and terrestrial ecosystems. Their inherent capacity to fix atmospheric nitrogen in the presence of nitrogenase also makes them ecologically important for rice-growing countries, where they contribute to rice-field fertility as a natural biofertilizer. Cyanobacteria fix >35 million tons of nitrogen annually and play a significant role in the biogeochemical cycles of nitrogen, carbon, and oxygen [1].

Cyanobacteria are an immense source of several natural products with medicinal, industrial, and agricultural value. They are also used as an alternative source of natural chemicals in synthetic cosmetics and as conventional energy resources [2]. The use of certain cyanobacterial species as nonconventional sources of food and protein is promising [3].

In recent decades, the release of anthropogenic atmospheric pollutants, such as chlorofluorocarbons, chlorocarbons, organobromides, and reactive nitrogen species (RNS), including nitric oxide, nitrous oxide, and peroxynitrite, has caused the depletion of the ozone layer, so that increased solar ultraviolet-B radiation (UV-B, 280–315 nm) reaches the Earth's surface. Under clear skies, UV-B reaching temperate and equatorial latitudes can be 1.5–2 W m^{-2}, as compared with 50–60 W m^{-2} of UV-A and 500 W m^{-2} of photosynthetically active radiation (PAR) [4]. Climate change can alter UVR exposure levels in inland and coastal marine waters [5]. There is little doubt that the Montreal Protocol, signed in 1987, has been successful in banning ozone-depleting substances, and with evidence of increases in stratospheric ozone it has been predicted that UV-B irradiance will decline by 5–20% in mid to high latitudes and by 2–3% in low latitudes by the end of 21st century [6]. However, these projected figures should be scrutinized cautiously since UVR is also influenced by changes in global climate via e.g. changes in cloud cover, concentrations of air pollutant and aerosols. Thus, such interactions between ozone and climate change make forcasts of decreasing UV levels less uncertain, and emphasizes the need to continue monitoring of the effects of UVR on aquatic organisms and ecosystem.

The increased incidence of UV-B has generated tremendous concerns about its negative effects on terrestrial and aquatic ecosystems, where it affects cyanobacteria, phytoplankton, and macroalgae. Like all photosynthetic organisms, cyanobacteria depend on solar energy for their normal life processes and therefore cannot avoid harmful solar UVR in their natural, brightly lit habitats. Solar UV-B affects the DNA and protein structures of cyanobacteria, their pigmentation, and several key metabolic activities, including photosynthesis, N_2 fixation, CO_2 uptake, ribulose 1,5-bisphosphate carboxylase/oxygenase (RuBisCO) activity, cellular morphology, growth, survival, and buoyancy [7–14].

However, cyanobacteria are not defenseless against the adverse effects of solar UVR. They have evolved a number of defense strategies, including apoptosis (or programmed cell death, PCD), efficient DNA repair mechanisms, including photoreactivation, excision repair, recombinational repair, and the SOS response, the production of antioxidants, the biosynthesis of UV-absorbing compounds, such as MAAs and scytonemin, migration, and mat formation [15–18]. In this review, we summarize the effects of UV-B and the subsequent evolution of tolerance mechanisms in cyanobacteria.

2. Mechanisms of UV-B damage in cyanobacteria

2.1. Biomolecules

Proteins and nucleic acids are primary targets of UV-B radiation. Damage caused by UV-B to proteins and RNA and DNA has been observed in several species of cyanobacteria. Increased UV-B exposure induces a proportional reduction in the numbers and quantities of proteins in many cyanobacteria. Quantitative proteome analysis employing mass spectrometry is becoming a powerful tool for investigating the global change in gene expression at the protein level under steady-state and perturbed, including UVR, conditions.

In some cyanobacteria, the proteome based on the IPG-Dalt system, revealed three responses (repressed and/or degraded or unaffected), involving different proteins whose synthesis is altered following exposure to UV-B irradiation [19].

Proteins of 14.5–45 kDa were completely lost when *Nostoc carmium* and *Anabaena* sp. were exposed to UV-B for 90 or 120 min [12,13], whereas other proteins of approximately 55 and 66 kDa were unaffected, even after 120 min of UV-B irradiation. In *Nostoc commune* and *Scytonema* sp., the proteins disappeared completely, following 150 min exposure to UV-B [12,13] and, similarly, Kumar et al. [20] reported the complete loss of proteins of between 14.2 and 45 kDa from *Nostoc calcicola* after exposure to UV-B for 90 or 120 min. Using two-dimensional gel electrophoresis (2DE), Ehling-Schulz et al. found changes in the proteome of *N. commune* after treatment with UV-B radiation and reported that of the 1350 protein spots 493 were altered. According to the authors, this makes the UV-B stimulon the most complex of any so far described, and consist of an early shock response affecting 214 proteins and, a later, acclimatization response with 279 proteins. They concluded that these responses characterize two distinct and highly complex strategies of *N. commune* for protection against UV-B [21].

In a more recent study, Gao et al. investigated the cytoplasmic proteins that are responsive to UV-B in *Synechocystis* sp. PCC 6803. Using 2DE in combination with tandem mass spectrometric (MS/MS) analysis, they reported a dramatic proteomic response in at least 112 protein spots among which 66 were up-regulated and 46 were down-regulated after UV-B exposure [22]. The identified proteins were mainly involved in amino acid biosynthesis, photosynthesis and respiration, energy metabolism, protein biosynthesis and cell defence [22]. Interestingly novel proteins not previous related to UV-B stress were indentified and indicates the complex nature of the functional network employed by cyanobacteria in response to UVR exposure [22].

Immunoreactions to whole-cell proteins using antibodies directed against D1 (PsbA) revealed protein loss in *Synechococcus* sp. WH8102 after UV exposure for 5 h [20]. After UV-B radiation and high light treatment, the total protein profile of *Nostoc spongiaeforme* and *Phormidium corium* was altered both qualitatively and quantitatively [23]. Similarly, UV irradiation repressed the 20-kDa and 22-kDa proteins in the sodium dodecyl sulfate (SDS) protein profile of *Lyngbya aestuarii* cells [24]. However, irradiation with UV-B for 6–24 h led to the overproduction of proteins of 84, 73, 60, 46, 40, and 37 kDa. SDS-polyacrylamide gel electrophoresis (PAGE) analysis of the total proteins of *Aulosira fertilissima* cells also showed a decreasing protein content as the period of exposure to UV-B increased.

DNA is an important molecule whose stability is essential for the proper functioning and existence of all living systems. UVR adversely affects genomic function and fidelity because native DNA molecules directly absorb UV-B radiation [25]. UV-B radiation can alter the normal state of life by inducing DNA strand breaks and a variety of mutagenic and cytotoxic DNA lesions, including cyclobutane-pyrimidine dimers (CPDs), 6-4 photoproducts (6-4PPs), and their Dewar valence isomers, which disrupt genomic integrity [16]. UVR-induced DNA degradation has been confirmed in several unicellular and filamentous cyanobacterial species. The UV-induced formation of thymine dimers (T<>T) has been observed in a number of rice-field cyanobacteria, such as *Anabaena* sp., *Nostoc* sp., and *Scytonema* sp. [26,27]. The frequency of thymine dimers increased as UVR exposure continued. Gao et al. [7] reported temperature- and biomass-dependent CPD formation under UV stress in the economically important cyanobacterium, *Arthrospira platensis*. Rastogi et al. recently reported UV-induced DNA damage in the cyanobacterium *Anabaena variabilis* PCC7937 [28] and UV-induced DNA degradation has also been demonstrated in the unicellular cyanobacterium *Synechocystis* PCC 6308 [29]. Using a polymerase chain reaction (PCR)-based assay of DNA damage, Kumar et al. observed a hypochromic effect on genomic DNA in the cyanobacterium *Anabaena* strain BT2 after UVR exposure [30].

UV-B can damage DNA by the formation of reactive oxygen species (ROS) [31]. A fluorimetric analysis of DNA unwinding by He and Häder quantified ROS-induced DNA strand breaks after UV exposure in the cyanobacterium *Anabaena* sp. [32]. UV-B-induced ROS [33] and DNA lesions (CPDs and 6-4PPs) can cause primary and secondary breaks, respectively. These lesions are commonly associated with transcription/replication blockage, which can lead to DNA double-stranded breaks at collapsed replication forks in CPD-containing DNA [15]. Recently, UVR-induced delay in chromosomal replication was observed in light/dark-synchronized cells of the marine cyanobacterium *Prochlorococcus marinus* PCC9511. This delay seemed to be linked to the strong downregulation of genes controlling DNA replication (*dnaA*) and cell division (*ftsZ*, *sepF*) [34].

UVR might affect cellular lipids and/or fatty acids and thereby disrupt the cells' integrity. The peroxidation of polyunsaturated fatty acids (PUFA) induced by UV-B radiation via oxidative damage has been observed in the cyanobacterium *Anabaena* sp. [35]. Differential lipid peroxidation in response to UV-B stress was also observed in three cyanobacterial species, *Nostoc muscorum*, *Plectonema boryanum*, and *Aphanothece* sp. Marked increases in the malondialdehyde (MDA) content of these three species (10%, 7%, and 3%, respectively) were observed after UV-B exposure for 15 min, indicating enhanced lipid peroxidation in these organisms [14]. Chris et al. [36] also observed an increase in MDA content in *Cylindrospermum* sp. following UV-B exposure, and a 73% increase in MDA formation was observed in the marine cyanobacterium *P. corium* after 6 h of UV-B exposure [23]. This increase in MDA following lipid peroxidation in cyanobacteria results from the oxidative degradation of PUFA in the cell membranes [37]. The fatty acid composition of the cyanobacterium *Spirulina platensis* after UV-B radiation was 23.5% saturated fatty acids (SFA) and 76.4% monounsaturated fatty acids (MUFA) and PUFA, whereas in UV-B-untreated *S. platensis*, SFA was 46.6% and MUFA and PUFA combined were 53.3% [38]. A large UV-B-induced reduction in SFA was also observed in the freshwater cyanobacterium *N. spongiaeforme* [23].

2.2. Biochemistry and physiology

Several studies have identified diverse effects of UVR on the pigmentation and photosynthetic parameters/performances of cyanobacteria. The pigments of the cyanobacteria include chlorophyll *a*, carotenoids, and phycobiliproteins, such as phycoerythrin (PE; λ_{max} 540–570 nm), phycoerythrocyanin (λ_{max} 560–600 nm), phycocyanin (PC; λ_{max} 610–620 nm), and allophycocyanin (APC; λ_{max} 650–655 nm), which harvest solar radiation. Among these pigments, the phycobiliproteins are the major photosynthetic accessory pigments of the cyanobacteria. They assemble into supramolecular light-harvesting complexes called "phycobilisomes", which are regularly arranged on the stromal surfaces of the thylakoid membranes.

UV-B radiation photobleaches photosynthetic pigments, such as chlorophyll *a*, carotenoids, and phycobiliproteins. A reduction in phycobiliprotein content and the disassembly of the phycobilisomal complexes following UV-B irradiation have been reported in many cyanobacteria.

The patterns of the fluorescence emission spectra of the phycobiliproteins after UV-B irradiation suggest that the energy transfer from the accessory pigments to the photosynthetic reaction center is impaired [39]. Phycobilisome disintegration was observed, followed by PC and PE bleaching, after the exposure of cyanobacterial cells to intense UV-B radiation [40]. An SDS-PAGE analysis of PC and associated linker polypeptides from *Anabaena* sp. revealed the loss of the αβ monomers of PC and rod-core and core-membrane linker polypeptides after 60 min of UV-B irradiation [41]. Rinalducci et al. [42] investigated the effects of UV-B radiation (1.3 W m^{-2}) on the light-harvesting apparatus of the cyanobacterium *Synechocystis* 6803 and found the rapid destruction of β-PC, with less damage to other biliproteins (α-PC, α-APC, and β-APC).

As well as the phycobiliproteins, UV-B radiation affects the chlorophyll and carotenoid contents of cyanobacteria. The photosynthetic pigments were completely bleached after 2–3 h of UV-B irradiation (5 W m^{-2}) in the rice-field cyanobacterium *A. fertilissima* [25]. In *N. muscorum*, a significant reduction in photosynthetic pigments was observed after 35 and 70 min of UV-B exposure (3.5 W m^{-2}). However, after 70 min of exposure, PC, carotenoids, and chlorophyll *a* were reduced by 86.4%, 81.25%, and 76.85%, respectively [43]. UV-B-induced thylakoid membrane distortion, with reduced chlorophyll *a* content, was observed in the cyanobacterium *S. platensis* [38]. In the marine cyanobacterium *Phormidium tenue*, the levels of the photosynthetic pigments chlorophyll *a*, myxoxanthophylls, and β-carotene

decreased by 74%, 81%, and 86%, respectively, after 6 h of UV-B irradiation (8 W m^{-2}) [44].

The consequences of UVR for the photosynthetic function of cyanobacteria have been extensively documented in terms of the diminution in chlorophyll *a* fluorescence, CO_2 uptake, RuBisCO activity, and O_2 evolution. UV-B exposure dramatically reduced the maximal quantum efficiency of photosystem II (PSII; F_v/F_m, the ratio of variable fluorescence to maximum fluorescence) in *Microcystis* spp. [45] and in the desert cyanobacterium *Scytonema javanicum* [46]. A similar reduction in the effective photochemical quantum yield has been observed in four species of cyanobacteria exposed to UVR: *Anabaena* sp., *Nostoc* sp., *A. platensis*, and *Microcystis* sp. [47]. However, UV-B had little effect on nonphotochemical quenching (NPQ) in *Microcystis* spp., indicating the inability of cyanobacterial PSII to dissipate high UV-B excitation energy [45]. Cockell and Rothschild described the effects of UVR on reducing the availability of adenosine triphosphate (ATP) and nicotinamide adenine dinucleotide phosphate ($NADPH_2$) [48]. This reduction diminished the CO_2-fixing capacity and overall primary productivity of cyanobacteria in microbial mats. Elevated levels of UV-B affect cyanobacterial photosynthesis, and may also affect their inorganic carbon concentration mechanisms (CCMs). However, while there are many studies on algae on the effects of UV-B on CCMs, there is a dearth of information on how UV-B influences the affinity for dissolved inorganic in cyanobacteria [49]. In a study on the operation of CCMs in *Microcystis aeruginosa*, Song et al. found little difference in the rate of total inorganic carbon uptake between controls and UV-B treated samples, although UV-B radiation did have differential effects on various inorganic carbon transporters [50]. In addition, the decrease in the number of carboxysomes was greater in UV-B treated cells than in controls. Exposure of *Anabaena* BT2 cultures to 1 h of UV-B at 0.4 W m^{-2} caused 60% reduction in ^{14}CO uptake and RuBISCO activity [9]. The photosynthetic enzyme RuBisCO can undergo several modifications, including photodegradation, fragmentation, denaturation of the polypeptide chains, changes in the active site, and increased the solubility of the membrane protein [9].

Recent studies suggest that PSII is more sensitive to UV-B exposure than PSI, and that the oxygen-evolving complex of PSII is the most important target of UV-B damage in cyanobacteria [51]. Zhang et al. recently found marked reductions in oxygen evolution (33–38% relative to the control) in two *Microcystis* strains under 0.372 W m^{-2} UV-B for four days, and the recovery rates of photosynthetic activity after UV-B treatment were lower in cyanobacteria than in the green alga *Chlamydomonas microsphaera* [45]. Furthermore, a severe reduction in the O_2-evolving activity of *Arthrospira* (*Spirulina*) *platensis* (56% after 3 h of UV-B) was accompanied by a significant loss of *de novo* synthesis of D1 protein (up to 40% of the initial value) at the PSII level [52]. The D1 and D2 polypeptides, the major constituents of the PSII reaction centers, were also degraded, even after the exposure of cyanobacteria to intermediate levels of UV-B radiation [52]. After short-term exposure (5 h) to UV (4.3 W m^{-2} UV-A and 0.86 W m^{-2} UV-B), a dramatic reduction in the amount of D1 protein was observed, with the rapid photoinactivation of the PSII reaction centers in the cyanobacterium *Synechococcus* sp. WH8102 [19]. It has been suggested that D1 protein degradation is accompanied by the disruption of the N-terminal domain of the anchor linker polypeptide L_{CM}, which in turn leads to the disassociation of the phycobilisome complex from the thylakoid membrane. The genes encoding the components of the phycobilisome, including the α-subunits of all the phycobiliproteins and phycoerythrin linker polypeptides, are all downregulated in response to UVR [19], and Sah et al. suggested that UVR affects L_{CM} in the cyanobacterium *Synechococcus* PCC 7942 [53]. UV-B radiation also affects some families of transcripts, including mRNAs that specify proteins involved in light harvesting and photosynthesis [54].

UV-B radiation can directly or indirectly affect the process of N_2 fixation. The key N_2-fixing enzyme, nitrogenase, is highly sensitive to UVR. For example, in *N. muscorum*, nitrogenase activity was inhibited by almost 55% after exposure to UV-B (3.5 W m^{-2}) for 4 min while after 16 min of UV-B exposure (2.5 W m^{-2}) complete loss of activity was recorded [43]. Similarly, complete loss of nitrogenase activity has been reported in several rice-field cyanobacteria, including *Anabaena* sp., *Nostoc* sp., *Calothrix* sp., and *Scytonema* sp., after 25–40 min of UV-B exposure (2.5 W m^{-2}) [8]. General reductions in NH_4^+ uptake and in the activities of nitrogenase, glutamine synthetase, and ATPase were reported in the cyanobacterium *Anabaena doliolum* after UV-B exposure, although significant increase in NO_3 uptake and nitrate reductase acticity were observed [55].

In general, the total annual nitrogen input attributable to biological nitrogen fixation by cyanobacteria is around 80%, with plants contributing up to 20% [56].

2.3. Morphology and cellular differentiation

Cyanobacteria exhibit a number of metabolic and developmental photoresponses that can be affected by UVR. Gao et al. observed a significant disruption of the differentiation of heterocysts and a reduction in trichome length of up to 49% in the cyanobacterium *Anabaena* sp. PCC7120 after UV-B exposure [57]. Sinha et al. also investigated the effects of artificial UVR (5 W m^{-2}) on heterocyst differentiation in four cyanobacterial strains (*Anabaena* sp., *Nostoc* sp., *N. carmium*, and *Scytonema* sp.) isolated from rice paddy fields in India and found that cellular exposure to UVR significantly affected the differentiation of vegetative cells into heterocysts [10]. Furthermore, changes in the carbon/nitrogen ratio following UV-B exposure may also be responsible for the altered spacing pattern of the heterocysts in the filament [10]. UV-B exposure delayed the differentiation of vegetative cells into heterocysts and akinetes in *Anabaena aequalis* [58]. Because heterocysts lack RuBisCO, they cannot fix CO_2 directly, but are dependent on vegetative cells to supply fixed carbon and to sustain N_2 fixation. N_2 is assimilated via the coupled glutamine c–glutamate synthase pathway to form glutamine and glutamate, which are then exported to the vegetative cells. Consequently, any change in the balance between heterocysts and vegetative cells could have a detrimental effect on survival.

The filaments of the cyanobacterium *Anabaena flos-aquae* were broken by UVR [13]. Cells in the trichome of the estuarine cyanobacterium *L. aestuarii* coiled and then formed small bundles in response to UV-B irradiation [24]. A natural level of solar UVR breaks and alters the spiral structure of *A. platensis* [13]. The exact mechanisms of cell/filament breakage are unknown, but UVR induces higher ROS accumulation and results in spiral breakages by oxidizing the sheath or cell membrane lipids in *A. platensis* [59]. Rastogi et al. recently proposed that UVR-induced breakage of the filaments of *A. variabilis* PCC 7937 with ROS production was the inductive agent for filament fragmentation [33]. However, the filament fragmentation of *A. variabilis* may be the result of lipid peroxidation and the selective lysis of damaged cells.

2.4. Motility and orientation

Motility and orientation are important avoidance mechanisms that protect cyanobacteria from the damaging effects of UVR and high light intensity. UVR severely affects the percentage of motile filaments and impairs the linear velocity of cyanobacterial cells, resulting in an impaired ability to escape harmful UVR. The effects of tropical solar radiation on the motility of certain cyanobacteria,

such as *A. variabilis*, *Phormidium uncinatum*, and *Oscillatoria tenuis*, were studied in Ghana, and a significant reduction in the percentage of motile filaments was observed after short-term (10–30 min) exposure to unfiltered solar radiation (134 klx, circa 1634.8 W m^{-2}) [59]. Similarly, *Oscillatoria salina* filaments ceased gliding within 16, 5, 3, and 1 h after irradiation with 0.96–3.84 kJ m^{-2} UV [60]. The removal of UVR with long-pass or band-pass filters resulted in the increased motility of these cyanobacteria, supporting the notion that UV radiation severely affects their gliding movement [59]. Advanced genetic studies in *Synechocystis* sp. PCC 6803 have indicated that the product of the pteridine glycosyltransferase (PgtA) enzyme, cyanopterin, is involved in the inhibition of movement by sensing UV radiation [61].

UV-B levels as low as 200 μmol m^{-2} m^{-1} (2 h exposure) can significantly impair motility and photosensory responses in cyanobacteria [62]. Yet, despite its damaging effects, UV radiation may play a role as an environmental cue for avoiding UV-induced damage. For example, when cells of *Microrocoleus chthonoplastes* were exposed to PAR (200 μmol m^{-2} m^{-1}), UV-A (3.9–4.8 μmol m^{-2} m^{-1}) and UV-B (0.98–2.2 μmol m^{-2} m^{-1}) separately, UV-B had a 100-fold and 20-fold greater effect than PAR and UV-A, respectively of inducing vertical migration, as a protective mechanism against intense solar radiation [63].

3. UV stress tolerance and adaptation in cyanobacteria

Cyanobacteria have a range of mechanisms for coping with the damaging effects of UVR. Different species of cyanobacteria vary widely in their tolerance of UVR. They have acquired a variety of defense strategies that allow them to survive and grow in adverse environments with high UV-B fluxes (Fig. 1). These strategies include avoidance, the scavenging of ROS by enzymatic/nonenzymatic antioxidant molecules, the synthesis of UV-absorbing/screening compounds, such as MAAs and SCY, the repair of UV-induced DNA damage, and protein resynthesis. In the following section, the defense/tolerance mechanisms adopted by cyanobacteria under adverse UVR conditions are discussed.

3.1. Avoidance

As a first line of defense against the elevated solar UVR in their natural, brightly lit habitats, a number of cyanobacteria have developed avoidance mechanisms, such as migration from high to low UVR levels, mat formation, morphological transformation, and the synthesis of extracellular polysaccharides (EPS). The upward and downward migration patterns of cyanobacteria may be closely linked to the daily changes in incident light intensity. Motile species of cyanobacteria can move deeper into the water column to escape high UV levels [64]. There is some evidence that low-intensity UV-A and/or UV-B radiation acts as a cue controlling vertical migration [65]. The cyanobacterium *Microcoleus chthonoplastes* in the microbial mats of Lake Sinai, Egypt, shows the highest incidence of migration in response to UV-B compared to UV-A or photosynthetically active radiation (PAR) [63]. The gliding movement of two cyanobacterial species, *Oscillatoria cf. laetevirens* and *Spirulina cf. subsalsa*, which occur in hypersaline ponds near Guerrero Negro, Mexico, was monitored under natural solar irradiance [66]. These cyanobacteria were shown to protect their

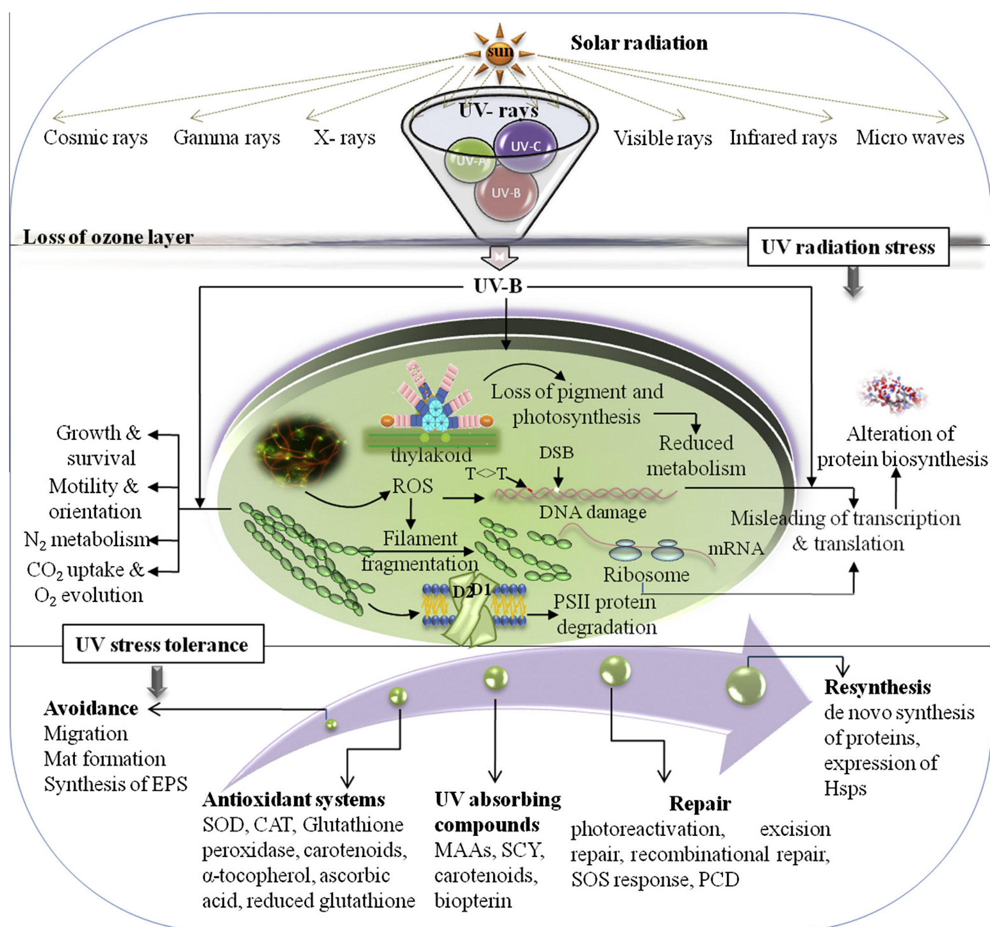

Fig. 1. A proposed model of the long-term UV-B stress responses in cyanobacteria (for details, see text).

photosynthetic machinery from UVR by gliding vertically downward. Ramsing and Prufert-Bebout reported the downward movement of a motile Oscillatoriales from microbial mat surfaces into the mat matrix or into soft sediments during periods of high insolation [67]. Such upward and downward migration was also monitored in the cyanobacterium *Oscillatoria* sp. in a hypersaline microbial mat on Antarctica's McMurdo Ice Shelf [68]. Thus, UVR influences the migratory behavior of motile cyanobacteria in microbial mats. However, in the mat on the McMurdo Ice Shelf, two closely related cyanobacterial species, *Phormidium murrayi* and *Oscillatoria priestleyi*, showed considerable differences in their ability to escape the damaging effects of UVR [63].

Populations of different species/strains of cyanobacteria form thick mats, which can be their primary way of avoiding harmful solar radiation [17]. However, the compositions of cyanobacterial mats vary under different environmental conditions and in different substrata, as do the abilities and properties of the colonizing species. In general, large filamentous cyanobacterial species colonize first, presumably because they have thick extracellular sheaths or mucus layers. Sutherland recently studied microbial mats sampled at 13 separated ponds on the McMurdo Ice Shelf, Antarctica, to examine the microbial mat communities responses to shifts in deterministic processes [69]. All the ponds were dominated by filamentous cyanobacteria of the order Oscillatoriales, whereas diatoms comprised only 10–15% of the community. Compared to aquatic systems, terrestrial habitats are more favorable for mat formation because of periodic long-term desiccation and higher UVR [70]. Mat formation by different taxa is considered a cooperative course of action in which the participating microorganisms benefit each other by the release of photoprotective substances [71].

The cyanobacterium *Microcoleus lyngbyaceus* formed an optimal mat after surface illumination of 1 klx (4 W m^{-2}) at a silt-depositing freshwater site in England [72]. Phoenix et al. found that cyanobacterial mats enclosed in amorphous silica matrices are protected from lethal UVR [73]. In the presence of UV-B radiation, the spiral structure of the cyanobacterium *A. platensis* is more compact, resulting in self shading, an effective protective mechanism against UVR [13].

3.2. Enzymatic/nonenzymatic antioxidant systems

Cyanobacteria have developed certain protective mechanisms that permit the optimal use of captured light energy while avoiding oxidative damage from potentially harmful ROS, including the superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), the hydroperoxyl radical (HO_2^-), and the hydroxyl radical (OH^-), induced by high irradiance. To counter this oxidative stress, cyanobacteria have evolved complex antioxidant systems based on low-molecular-weight scavengers and specifically adapted enzymes as a second line of defense against UVR. These mechanisms involve enzymatic and nonenzymatic antioxidants. In photosynthetic organisms, including cyanobacteria, superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), and the enzymes involved in the ascorbate–glutathione cycle, such as ascorbate peroxidase (APX), monodehydroascorbate reductase, dehydroascorbate reductase, and glutathione reductase (GR), are the major enzymatic antioxidants; carotenoids, α-tocopherols (α-TOC; vitamin E), ascorbic acid (ASA; vitamin C), and reduced glutathione are nonenzymatic antioxidants.

SOD, one of the most important antioxidant molecules, can detoxify superoxide radicals within cells. SOD exists in four different metalloforms, according to the nature of the catalytic metal (i.e., FeSOD, MnSOD, Cu/ZnSOD, and NiSOD) and protects different cellular proteins against oxidative stress. In the cyanobacterium *N. commune*, active Fe-containing SOD accumulates under desiccation and rehydration during UV-A and UV-B irradiation [21]. The following SODs have been found in several cyanobacteria: FeSOD and MnSOD in *Anabaena* sp. (*Nostoc*-type); an MnSOD in *Cyanothece*, CCY 0110; only FeSOD in *Synechococcus* sp.; and MnSOD and NiSOD in *Trichodesmium* sp. [74]. A genomic analysis showed that FeSOD and MnSOD occur in the higher orders of cyanobacteria, Cu/ZnSOD is rare in cyanobacteria, and NiSOD is the only SOD found in the primitive cyanobacteria [75]. The primitive unicellular *Prochlorococcus* expresses only NiSOD, whereas the developed middle-order forms of cyanobacteria express a combination of Fe–NiSOD and Fe–MnSOD [75]. Priya et al. recently characterized the MnSOD from the marine cyanobacterium *Leptolyngbya valderiana* BDU20041 [76]. In another cyanobacterium, *Anabaena* PCC 7120, MnSOD is involved in the acclimation of the strain to high light levels and MnSOD is required for the protection of nitrogenase from ROS [77]. Increased SOD and APX activities were observed under high-intensity light treatments in the freshwater cyanobacterium *N. spongiaeforme* and the marine cyanobacterium *P. corium* [23]. SOD, APX, and nonenzymatic compounds such as ASA, carotenoids, and α-TOC were produced in *A. doliolum* in response to UV-B-induced oxidative stress and other abiotic factors [78].

SOD scavenges superoxide radicals and converts them to H_2O_2, which is then converted to H_2O and O_2 via a combined catalase–peroxide system [79]. Miyake et al. described the scavenging system for H_2O_2 in cyanobacteria with reference to the acquisition of APX during their evolution [80]. Some species of cyanobacteria lack APX as an H_2O_2-scavenging enzyme. Therefore, cyanobacteria can be divided into two groups: one uses APX and CAT to scavenge H_2O_2, and the other uses only CAT [81]. Three types of CAT proteins have been identified based on their amino acid sequence similarities and physical and chemical properties: monofunctional heme-containing CATs, bifunctional heme-containing CAT–peroxidases, and nonheme-manganese CATs. Analyses of genome sequences for CAT-orthologues revealed their presence in 20 cyanobacterial genomes [82]. Tichy and Vermaas proposed a protective role for CAT–peroxidase against environmental H_2O_2 production in the cyanobacterium *Synechocystis* sp. PCC 6803 [83]. However, this protective role was most apparent at high cyanobacterial densities.

Glutathione, another component of the cyanobacterial antioxidant system, is a small ubiquitous molecule that plays an important role in several cellular processes, in addition to its role as an antioxidant and in the maintenance of the cellular redox homeostasis [84]. Unlike the roles of glutathione in heterotrophic organisms, such as yeast and *Escherichia coli*, very little is known about the roles of glutathione in photosynthetic organisms, including cyanobacteria. Glutathione metabolism probably evolved with the advent of oxygenic photosynthesis in cyanobacterial ancestors [85]. Compared with plants, cyanobacteria have smaller gene families related to glutathione metabolism, making them excellent candidates for the study of glutathione metabolism in photosynthetic organisms [86]. Cameron and Pakrasi recently investigated the role of glutathione in the acclimation of the cyanobacterium *Synechocystis* sp. PCC 6803 to environmental and redox perturbations [87]. Glutathione protects the thiol groups in various enzymes, and is involved in the regeneration of α-TOC and ascorbate through the glutathione–ascorbate cycle. The genome of *Anabaena* sp. contains an open reading frame (ORF) with homology to a novel hybrid form of thiol peroxidase fused to a glutaredoxin domain [88]. Glutathione-dependent thiol peroxidase is an adaptive strategy in *Anabaena* sp. that efficiently combats H_2O_2. A functional analysis of two reduced NADPH-dependent GPX-like proteins during the progress of oxidative stress in the cyanobacterium *Synechocystis* PCC 6803 revealed that GPX-1 and GPX-2 are essential for the removal of lipid hydroperoxides under normal and stressed conditions [89].

GR is a key enzyme in the glutathione–ascorbate cycle, functioning in peroxide scavenging and protecting against other oxidative processes in cyanobacteria. Ascorbate directly quenches ROS, regenerates α-TOC, and acts as a substrate in the violaxanthin de-epoxidase and APX reactions [90]. The exogenous addition of ASA and *N*-acetyl-l-cysteine (NAC) reduces UVR-induced oxidative damage, including chlorophyll bleaching, damage to the photosynthetic apparatus, lipid peroxidation, and DNA strand breaks, in the cyanobacterium *Anabaena* sp. [32]. Wang et al. also reported the involvement of antioxidant systems, such as NAC and ASA, in the protection of the cyanobacterium *Nostoc* sp. against UV-B radiation [91]. In the cyanobacterium *Synechocystis* PCC 6803, two NADPH-dependent GSH-Px-like proteins are essential in protecting membranes from lipid peroxidation [89]. Zhao et al. identified a different type of peroxidase, called rubrerythrin homologue (RbrA), in *Anabaena* sp. PCC 7120, which protects its nitrogenase from oxidative stress [92].

The synthesis of carotenoids by *M. aeruginosa* increases under prolonged UV-B exposure [47]. Kelman et al. found that carotenoids provide the major antioxidant defense in the marine cyanobacterium *Trichodesmium* sp. [93]. Long-term exposure to high levels of natural or artificial UVR increases the carotenoid/chlorophyll *a* ratio, a prerequisite for UV protection [94]. Several studies of the biosynthetic pathways of some carotenoids in cyanobacteria have recently been published [95,96]. Cyanobacteria produce a wide variety of carotenoids, including myxoxanthophyll, β-carotene, and its derivatives (including zeaxanthin and echinenone). Nonenzymatic antioxidant carotenoids, localized in the outer cellular membrane and the thylakoid membranes, act as light-harvesting pigments in photosynthesis and protect cyanobacterial cells against photooxidative damage by absorbing triplet-state energy from chlorophyll *a* to dissipate any excess photochemical energy and quench singlet oxygen radicals. Outer-membrane-bound carotenoids provide a rapid SOS response to counteract severe cell damage. An analysis of cyanobacterial envelope membranes demonstrated that xanthophylls are the predominant carotenoids, whereas β-carotene is predominantly located in the thylakoids [97]. The cyanobacterium *Synechococcus* sp. PCC 7002 produces six different xanthophyll carotenoids, zeaxanthin, cryptoxanthin, myxoxanthophyll (i.e., myxol-2′-fucoside), echinenone, 3′-hydroxyechinenone, and synechoxanthin, and tolerates many environmental stresses, including high light irradiance. Significantly increased levels of the outer-membrane carotenoids echinenone and myxoxanthophyll were found in the cyanobacterium *N. commune* DRH1 after UV-B irradiation for several hours [94]. Similarly, myxoxanthophyll and echinenone are the predominant pigments in the outer membrane of *Synechocystis* sp. strain PCC 6714 [97]. The photosynthetic activity of the cyanobacterium *Synechococcus* sp. PCC 7942 was more tolerant of UV-B radiation when the amounts of endogenous carotenoids were increased [98]. Zeaxanthin is particularly important for photoacclimation in *Synechococcus* PCC 7942 during UV-B stress [98]. A mutant of *Synechocystis* PCC 6803 deficient in zeaxanthin synthesis was more sensitive to high light and oxidative stress treatments than the wild type [99]. Zhu et al. recently suggested that xanthophylls play regulatory roles in thylakoid biogenesis, and that all xanthophylls participate in preventing ROS/RNS accumulation and contribute to the protection of cells from photooxidative stress [96]. Cyanobacteria also produce some unique types of xanthophylls, such as ketocarotenoids and glycosides [100]. Ehling-Schulz et al. have also demonstrated these carotenoids in the cyanobacterium *N. commune* DRH1 after UV-B irradiation [94]. In some Antarctic cyanobacterial mats dominated by *N. commune* and *Oscillatoria* sp., there are high concentrations of carotenoids, such as myxoxanthophyll and canthaxanthin, which create a bright orange or pink color and act as photoprotectants [60]. The occurrence of orange carotenoid protein (OCP) and its role in photoprotection have been reported in various cyanobacteria [101]. Boulay et al. also recently identified fluorescence recovery protein (FRP) in *Synechocystis* PCC 6803, which mediates the recovery of the full antenna capacity when irradiance decreases [102]. FRP is a 14-kDa protein encoded by the *slr1964* gene; homologues of this gene are present in all OCP-containing strains of cyanobacteria. Schagerl and Müller investigated the adjustments in chlorophyll *a* and the carotenoid compositions in response to UVR in four freshwater cyanobacteria; the highest induction was found in the carotenoid–glycosyl myxoxanthophyll levels [103]. They therefore suggested that the nature of the carotenoids overproduced in response to high irradiance varies from one cyanobacterium to another. Myxoxanthophyll is known to be the most effective carotenoid in protecting *Synechocystis* PCC 6803 from peroxidation [104].

Carotenoids might also augment the peroxy-radical-scavenging capacity of α-TOC [105]. Tocopherols are lipid-soluble organic molecules exclusively synthesized by oxygenic phototrophs, such as plants, green algae, and some cyanobacteria. However, TOC-deficient mutants of *Synechocystis* PCC 6803 can cope with high-light stress and $^1O_2$ accumulation, indicating that tocopherols are not the only molecules that protect photosystems from peroxy radicals [106]. Furthermore, simultaneous changes in tocopherols and carotenoids affected the high-light-stress tolerance of the cyanobacterium *Synechocystis* sp., indicating that the functions of these two antioxidants overlap. However, the elimination of tocopherols has surprisingly subtle effects on cyanobacterial tolerance of high light stress [107]. Yang et al. reported that α-TOC is essential for acquired chill-light tolerance in the cyanobacterium *Synechocystis* sp. PCC 6803 [108].

The presence of phenolic antioxidants is less well documented in microalgae than in terrestrial plants. However, several recent reports indicate that flavonoids, such as isoflavones, flavones, flavonols, and dihydrochalcones, occur in macroalgae and cyanobacteria [109]. Although the importance of phenolic compounds in the antioxidative protection of cyanobacteria has not yet been clearly demonstrated, the increases in phenolic substances in the microalgal biomass after exposure to UVR suggests that they play a role in the antioxidative response to UVR [109].

There have been a number of significant studies investigating the role of antioxidant enzymes in several organisms, but information on UV-B-induced antioxidant defenses in cyanobacteria is still sparse.

3.3. Synthesis of extracellular polysaccharides

Cyanobacterial EPS are generally high-molecular-mass heteropolysaccharides with erratic compositions and roles, depending on the microorganism and the environmental conditions. Pereira et al. recently reviewed cyanobacterial EPS, including their compositions and functions, factors affecting their synthesis, and the putative mechanisms of their biosynthesis [110]. The synthesis of EPS is also an important strategy used to avoid high-intensity UVR. The production of EPS varies among different species/strains of cyanobacteria, and even a single strain can produce different types of EPS at different growth stages [111]. Organisms that have extremely thick outer sheaths of EPS can better withstand high solar radiation and desiccated conditions. Cyanobacteria synthesize EPS in response to UV-B because EPS provides a matrix for MAAs and scytonemin (SCY) [94]. It is feasible that these pigments covalently link to glycan after they are secreted from the cell [112]. In the cyanobacterium *N. commune*, UV-B radiation stimulates the production of extracellular glycans, which might provide UV resistance by increasing the effectual path length for the absorption of radiation [97]. Investigation of UV-B-induced oxidative damage and the protective effects of EPS in the cyanobacterium *Microcoleus*

vaginatus, isolated from a desert crust, suggested that EPS provide significant protection against DNA strand breaks and lipid peroxidation by effectively eliminating UV-B-induced ROS [113]. The cyanobacterium *M. vaginatus* excretes large amounts of EPS into the culture medium, which create a boundary between the cells and the surrounding environment, protecting them against desiccation and UVR [113]. Li et al. recently revealed the free-radical-scavenging role of EPS from *N. commune* [114]. However, few studies have described the contribution of EPS excretion to enhancing UV-B tolerance in cyanobacteria.

3.4. Synthesis of UV-absorbing/screening compounds

An interesting property of several cyanobacteria is their capacity to overcome UVR toxicity using UV-absorbing/screening compounds as a third line of defense [17]. Mycosporines/MAAs and SCY are prominent photoprotectants that act against UV-B and/or UV-A radiation. Mycosporines/MAAs have been identified in taxonomically diverse organisms, including heterotrophic bacteria, lichens, cyanobacteria, fungi, micro/macroalgae, and several animals. The presence of MAAs in higher animals can be attributed either to their ingestion through food chain or to MAA synthesis by symbiotic algal partners. In contrast to MAAs, SCY is predominantly produced by cyanobacteria.

3.5. Mycosporines and MAAs

Mycosporines and MAAs are small (<400 Da), colorless, water-soluble compounds composed of a cyclohexenone or cyclohexenimine chromophore conjugated to the nitrogen substituent of an amino acid or its imino alcohol (Fig. 2). Commonly, the ring system includes a glycine subunit at the third carbon atom, although some MAAs contain sulfate esters or glycosidic linkages through the imine substituents. Differences between the absorption spectra of MAAs arise from variations in the attached side groups and nitrogen substituents. Strong UV absorption maxima (310–362 nm), high molar extinction coefficients ($\varepsilon = 28{,}100–50{,}000\ M^{-1}\ cm^{-1}$), photostability in fresh and saline water in the presence of photosensitizers, antioxidant properties, and resistance to several abiotic stressors (such as temperature, UVR, various solvents, and pH) indicate that MAAs are photoprotective compounds [115,116].

Shibata first reported the accumulation of large amounts of MAAs in cyanobacteria [117]. To date, a number of cyanobacteria have been reported to produce different MAAs in diverse habitats (Table 1). The photoprotective efficiency of MAAs depends on their position within the cell. MAAs effectively dissipate absorbed radiation as heat, without producing ROS [115]. They prevent three of every 10 photons from hitting cytoplasmic targets in cyanobacteria [118], and there is clear evidence that MAAs protect several

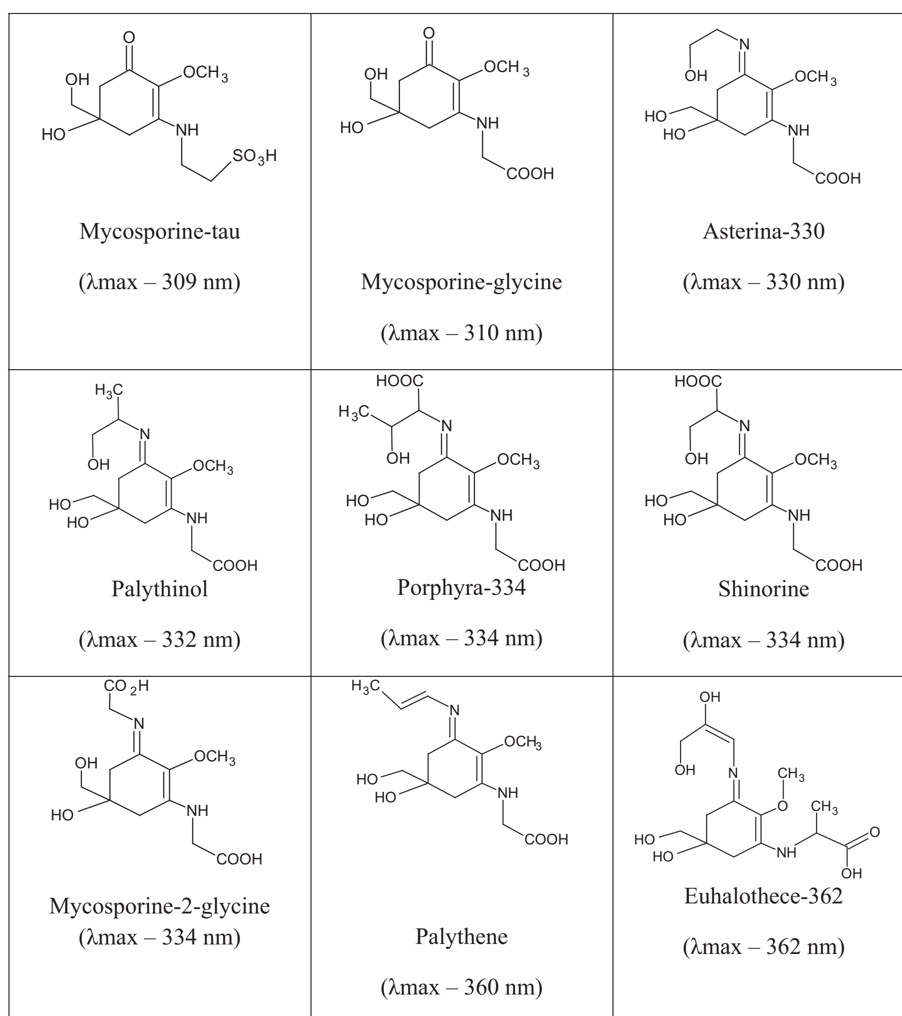

Fig. 2. Structure of some common MAAs found in cyanobacteria.

Table 1
Occurrence of MAAs in various species of cyanobacteria.

Organisms	MG	AS	PL	PR	SH	PE	E-362	M2G	M-tau	DL	M-343	References
Anabaena sp.	–	–	–	–	+	–	–	–	–	–	–	[185,131]
Aulosira fertilissima	–	–		+	+	–	–	–	–	–	–	[186]
Aphanothece halophytica	–	–	–	–	+	+	–	–	–	–	–	[187]
Aphanizomenon.flos–aquae	–	–	–	+	–	–	–	–	–	–		[188]
Calothrix sp.	+	–	+	–	+	–	–	–	–	–	–	[189]
Chlorogloeopsis sp.	+	–	+	–	+	–	–	–	–	–	–	[189,190]
Diplocolon sp.	+	–	–	–	–	–	–	–	–	–	–	[189]
Euhalothece sp.	–	–	–	–	–	–	+	+	–	–	–	[191,192]
Gloeocapsa sp.	+	+	+	–	+	–	–	–	–	–	–	[189,118,193]
Gloeothece sp.	+	–	–	–	–	–	–	–	–	–	–	[189]
Lyngbya aestuarii	–	+	–	–	+	–	–	–	–	–	–	[189,71]
Microcystis aeruginosa	–	–	–	+	+	–	–	–	–	–	–	[145]
Microcoleus chthonoplastes	–	–	–	–	+	–	–	–	–	–	–	[78,194]
Nodularia sp.	–	–	–	+	+	–	–	–	–	–	–	[123]
Nostoc commune	+	–	–		+	–	–	–	–	–	–	[195,196,123]
Nostoc harveyana	–	–	–	+	+	–	–	–	–	–	–	[123]
Phormidium tenue	–		–	–	+	–	–	–	–		–	[44]
Nostoc spumigena	–	–	–	+	+	–	–	–	–	–	–	[123]
Scytonema sp.	+	–	–	–	+	–	–	–	–	–	–	[94,189,197–199,123]
Synechococcus sp.	+	–	–	–	–	–	–	–	–	–	–	[189]
Synechocystis sp. PCC 6803	–	–	–	–	–	–	–	–	+	+	+	[200]

[M: mycosporine-like amino acids; MG: mycosporine-glycine; AS: asterina-330; PL: palythinol; PR: porphyra-334; SH: shinorine; PE: palythene; E362: euhalothece-362; M2G: mycosporine-2-glycine; M-tau: mycosporine-tau; DL: dehydroxylusujirene].

vital functions in phytoplankton from the effects of harmful short-wavelength radiation [119]. MAAs can also block the formation of UV-induced thymine dimers [120].

Until recently, MAA and mycosporine biosynthesis was thought to occur via the first part of the shikimate pathway in cyanobacteria and fungi: 3-dehydroquinate, formed during the early part of the shikimate pathway, acts as a precursor for the synthesis of fungal mycosporines and MAAs via gadusol or deoxygadusol [121]. However, Balskus and Walsh recently challenged the long-standing assumption that MAA biosynthesis involves an intermediate of the shikimate pathway [122]. A cluster of four genes present in the cyanobacterium *A. variabilis*, which produces the MAA shinorine, was found to be responsible for the conversion of the common pentose-phosphate-pathway intermediate sedoheptulose-7-phosphate to shinorine via 4-deoxygadusol [123]. In this process, the dehydroquinate synthase homologue Ava_3858 and the *O*-methyltransferase Ava_3857 convert the precursor into 4-deoxygadusol; the ATP-grasp homologue Ava_3856 then converts 4-deoxygadusol and glycine into mycosporine–glycine and a nonribosomal peptide synthetase-like enzyme. Finally, Ava_3855 attaches to mycosporine–glycine and serine to form shinorine (Fig. 3).

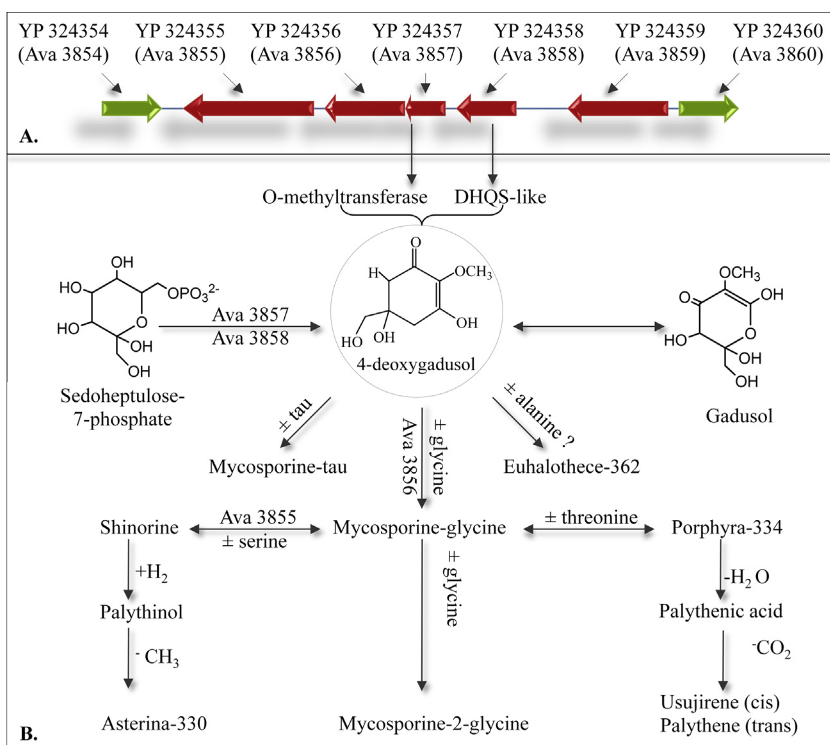

Fig. 3. (A) Proposed gene cluster for MAA biosynthesis reported in the cyanobacterium *Anabaena variabilis* PCC7937. (B) Possible pathway for the interconversion and/or accumulation of some MAAs found in cyanobacteria (adapted from [122,201]).

The UV-B-induced synthesis of shinorine and porphyra-334 (both with absorption maxima at 334 nm) has been reported in three filamentous and heterocystous cyanobacterial strains of *Nodularia*: *N. baltica*, *N. harveyana*, and *N. spumigena* [124]. The conversion of mycosporine–glycine into two MAAs, porphyra-334 and shinorine, in response to PAR and UVR was observed in the cyanobacterium *A. doliolum* [125]. Sulfur deficiency has been shown to regulate the synthesis and bioconversion of a primary MAA into a secondary MAA in the cyanobacterium *A. variabilis* PCC 7937 [126]. Several abiotic factors, such as different UVR wavelengths, desiccation, nutrients, salt concentrations, and light and dark periods, affect the production of photoprotective compounds in cyanobacteria. MAA synthesis is an energy-dependent process.

MAAs are multipurpose secondary metabolites that can be exploited biotechnologically in various ways. Oyamada et al. reported that three MAAs, shinorine, porphyra-334, and mycosporine–glycine, protect human fibroblast cells from UVR and promote their proliferation [127]. Recently, De la Coba et al. reported the capacity of these compounds to prevent UV-induced skin damage in vivo [116]. Thus, certain MAAs, including shinorine and porphyra-334, have been commercialized globally for the production of skin care and cosmetic products, such as Helioguard 365, M-Rose and Fikia (BeautyLine Ltd.).

3.6. Scytonemin

SCY is the most widespread and extensively characterized sunscreen pigment and is exclusively produced by cyanobacteria. It is a yellow–brown, lipid-soluble, dimeric compound composed of indolic and phenolic subunits, with a molecular mass of 544 Da. SCY was first identified by Nägeli in several terrestrial cyanobacteria [128]. The compound is located in the EPS sheath of some cyanobacteria, where it acts as a passive sunscreen to protect against UVR. Three new derivatives of SCY, dimethoxyscytonemin, tetramethoxyscytonemin, and scytonin, have been produced from organic extracts of *Scytonema* sp., collected on the Mitaraka massif, French Guyana [129]. The complexity of the SCY ring structures generates a specific pattern of UV absorbance [130]. SCY has an in vivo absorption maximum at 370 nm, and purified SCY has an absorption maximum at 386 nm, although it also absorbs significantly at 252, 278, and 300 nm. SCY allows cyanobacteria to survive lethal UV-A/B radiation in environments with intense sunlight [131]. SCY is highly stable, and it screens without any further metabolic investment, even after prolonged physiological inactivity. Therefore, it is a suitable compound to defend cyanobacteria against UVR when other protective mechanisms would be ineffective [132].

SCY biosynthesis probably involves tryptophan and tyrosine derivatives that absorb ambient UVR [133]. In stable-isotope-enrichment studies, Jones et al. monitored the incorporation of tyrosine and tryptophan, the aromatic amino acid-derived subunits, into SCY [133]. They also showed that the ketone carbon involved in the condensation of these two biosynthetic precursors derives from the tryptophan subunit. A gene cluster responsible for SCY production was identified in *Nostoc punctiforme* ATCC 29133, consisting of 18 unidirectionally transcribed ORFs (*NpR1276–NpR1259*), including eight genes involved in the biosynthesis of tryptophan and tyrosine [134]. The other genes showed no significant homology with any functionally characterized proteins (Fig. 4). Balskus and Walsh presented a probable route for SCY biosynthesis and identified the acyloin reaction as a key step in constructing the carbon framework of this ecologically and evolutionarily important pigment [135]. They identified two potential candidates (NpR1275 and NpR1276) as enzymes that participate in the early stages of SCY biosynthesis. These researchers further demonstrated that the NpR1274 enzyme encoded by the SCY

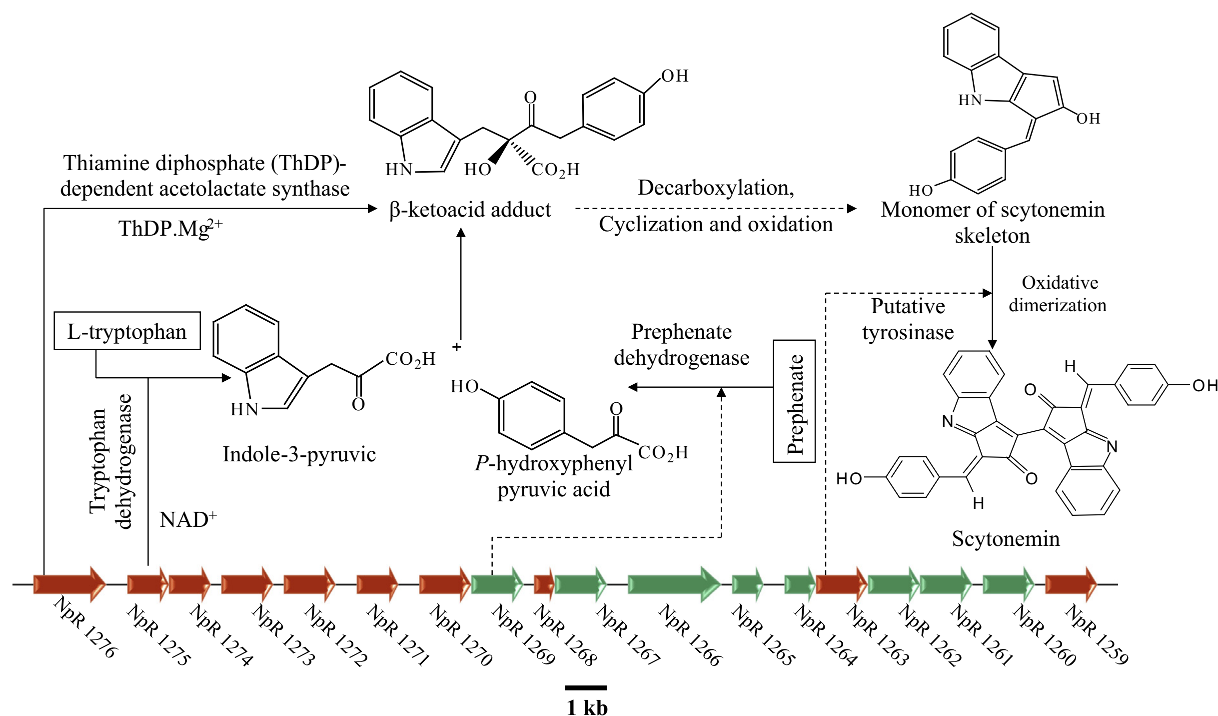

Fig. 4. Proposed biosynthetic pathway for scytonemin in the cyanobacterium *Nostoc punctiforme* ATCC29133 and the associated gene products (NpR1259–NpR1276). Most of the open reading frames (ORFs) in the gene cluster (*NpR1269* to *NpR1260*; green arrows) are predicted to be involved in the biosynthesis of an aromatic amino acid. The ORFs represented by red arrows (e.g., *NpR1276–Np1271*; *ScyA–F*) are predicted to be involved in SCY biosynthesis, although most of these ORFs encode proteins of unknown function. Continuous arrows signify gene products that have been functionally characterized, and broken arrows indicate the gene products that have not been functionally characterized (adapted from [201]).

cluster catalyzes the cyclization and decarboxylation of the NpR1276 product to form a ketone thereby yielding a cyclopentane [136]. The products of the ORFs of *NpR1263* and *NpR1269* have yet to be functionally characterized. The association of these genes and their roles in SCY biosynthesis are further supported by evidence that the transcription of each gene in the cluster increases after *N. punctiforme* ATCC 29133 is exposed to UV-A radiation [137]. Several cyanobacterial genomes across a number of cyanobacterial lineages have recently been investigated to identify the SCY biosynthetic gene cluster [137]. Some genetic variation exists between genome clusters, but the majority of these genes encode proteins with a high degree of amino acid sequence similarity, implying that SCY biosynthesis has evolved as a highly conserved process to defend cyanobacteria against UVR [138].

Other UV-absorbing compounds, in addition to MAAs and SCY, have been isolated from cyanobacteria. Biopterin glucoside, with absorption maxima at 256 and 362 nm, has been purified from a marine planktonic cyanobacterium, *Oscillatoria* sp., collected from the coastal areas of Japan [139]. Relatively large concentrations of pteridines have also been found in certain cyanobacterial species, including *Anacystis nidulans*, *A. variabilis*, *N. muscorum*, and *N. maseaum*. Ploutno and Carmeli reported that another novel UV-absorbing compound, prenostodione, from the cyanobacterium *Nostoc* sp. (TAU strain IL-235), has maximum UV absorption at 217, 230, 287, and 318 nm [140]. A large number of photoprotective compounds have been identified in cyanobacteria, but none has been chemically characterized. Therefore, much work remains to clarify the structures and functions of the photoprotective compounds in the cyanobacteria.

3.7. Expression of heat shock proteins (Hsps)

Hsps are a class of general stress proteins that play an important role in normal cellular functions and in cellular survival under several stress conditions, including UVR [141]. The expression of Hsps in response to UVR is assumed to be part of the endogenous UV response. Hsps increase the cell's resistance to stress by influencing the DNA repair mechanisms or the induction of apoptosis [142]. Small Hsps have protein-protective activity and the capacity to stabilize lipid membranes [143], and they are ubiquitous in the biological world. There is some evidence that physical interactions between small Hsps and thylakoid membrane/membrane proteins in cyanobacteria [144] confer ultrastructural stability on the thylakoids at high temperatures, and intense light, and under oxidative stress. A mutant small Hsp (Hsp17), with increased thylakoid association, increases the resistance of the cyanobacterium *Synechocystis* sp. PCC 6803 to UV-B damage [141]. Hossain and Nakamoto clarified a role of HtpG in the cyanobacterium *Synechococcus* sp. PCC 7942, suggesting that HtpG protects against the photooxidative stress caused by high irradiance, alone or in cooperation with other Hsps, and that it plays a direct or indirect role in the protection of PSII [144]. A gene encoding a small Hsp, *HspA*, is induced by peroxide in the cyanobacterium *Synechocystis* sp. strain PCC 6803, indicating that the encoded protein plays a role in defending the strain against oxidative stress [145]. However, the in vivo roles of small Hsps in cyanobacteria during oxidative stress remain to be clarified.

3.8. Repair and resynthesis of damaged DNA and proteins in cyanobacteria

The repair and resynthesis of UV-damaged biomolecules, such as DNA and proteins, are crucial if various organisms, including cyanobacteria, are to maintain their normal status. Several DNA repair mechanisms, including photoreactivation, excision repair, and recombinational repair, function to moderate UVR-induced damage in cyanobacteria (Fig. 4). However, the incidence of a particular repair pathway within the cell depends principally on the type and location of the lesion in the genome [146]. Biochemical and molecular studies of DNA repair mechanisms were recently reviewed by Rastogi et al., who showed that photoreactivation is one of the dominant repair mechanisms [15]. Photoreactivation can remove DNA lesions, such as CPDs or 6-4PPs, in the presence of the DNA photolyase enzymes CPD photolyase and 6-4 photolyase, respectively, using long-wavelength UV-A/blue light energy. Photolyases (45–66 kDa, 420–616 amino acids) are monomeric flavin-dependent repair enzymes that require two known cofactors: a catalytic cofactor, such as 5,10-methenyltetrahydrofolate (MTHF) [147], 8-hydroxy-5-deaza-riboflavin (8-HDF) [148], or flavin mononucleotide [149], and a light-harvesting cofactor, such as deprotonated reduced flavin adenine dinucleotide ($FADH^-$). Long-wavelength UV-A or blue light energy is absorbed by either MTHF or 8-HDF ($\lambda_{max} \sim 380$ and ~ 450 nm, respectively) and transferred to the catalytic cofactor $FADH^-$.

In its excited state, the flavin transfers an electron to CPD, splitting the cyclobutane ring. The electron is transferred back to flavin, generating the two canonical bases [15]. After the photolyase binds to CPD, the photoreactivation efficiency is extremely high; one dimer splits after the absorption of almost every blue light photon [150]. This photoreactivation process has been reported in several cyanobacteria, including *Synechocystis* sp. PCC 6803 [151], *Agmenellum quadruplicatum* [152], *A. nidulans* [153], *Gloeocapsa alpicola* (*Synechocystis* sp. PCC 6308) [29], *P. boryanum* [154], and *Anabaena* spp. [155]. Recently, Rastogi et al. reported the photoreactivation of UV-induced T<>TCPD in the cyanobacterium *Anabaena* sp. PCC 7937 [28].

The dark or excision repair pathway, in which damaged DNA is replaced by new undamaged nucleotides via the complementary DNA strand, also plays an important role in DNA repair. DNA glycosylases are among the key enzymes that can remove different types of modified bases. Some evidence supports the occurrence of excision repair in cyanobacteria [156]. The gene for the DNA repair enzyme formamidopyrimidine–DNA glycosylase was identified in the cyanobacterium *Synechococcus elongatus* [157]. UV-endonucleases have also been isolated from the unicellular cyanobacterium *Synechocystis* PCC 6308 [158]. In several cyanobacterial strains, sensitivity to UV irradiation increases in the presence of caffeine or acriflavine (an inhibitor of excision repair), providing indirect evidence of excision repair in cyanobacteria [160]. Moreover, an increase in the transcript levels of recA and a concomitant increase in the abundance of the corresponding 37–38-kDa polypeptide have been reported in *A. variabilis* following UV irradiation [159]. The *recA* gene encodes a DNA-dependent ATPase that binds to single-stranded DNA and promotes strand invasion and exchange between homologous DNA molecules [160]. The accumulation of massive amounts of DNA lesions within cells during different specific physiological responses can activate the SOS repair system, which has been well described in *E. coli* [161]. The SOS repair system is initiated by the interaction of two crucial proteins, RecA and the LexA repressor. The latter represses the expression of the SOS genes by binding to their promoters [161]. Li et al. recently analyzed the LexA regulons in cyanobacteria and found that in most cyanobacterial genomes, LexA appears to function as a transcriptional regulator of the key SOS response genes [162]. However, the SOS response mechanism in cyanobacteria is still to be characterized.

In addition to the aforementioned repair mechanisms, apoptosis (or PCD) can occur when a cell is damaged beyond repair, thereby protecting the organism at the expense of the individual cell. PCD has been described in various phytoplankton species [163], including cyanobacteria (e.g., *Trichodesmium* sp. and *Anabaena flos-aquae*) [164,165], green algae (e.g., *Dunaliella tertiolecta*), and

dinoflagellates (e.g., *Peridinium gatunense*) [166]. The freshwater cyanobacterium *Anabaena* activates PCD and increases general protease activity after exposure to univalent cationic salts [165]. In the nitrogen-fixing cyanobacterium *Trichodesmium* sp., high radiation, iron starvation, and oxidative stress induce PCD [164]. Caspase activity and reactivity to human anti-caspase 3 antibodies has also been reported in *Trichodesmium* sp. [164], and a number of genes encoding caspases (enzymes involved in PCD in eukaryotes) have been reported in the sequenced genome of *M. aeruginosa* [167]. Ross et al. showed that H_2O_2 induces PCD and catalase inhibits it in the cyanobacterium *M. aeruginosa*, implicating PCD in the response of this cyanobacterium to oxidative stress [168]. However, the exact mechanisms of PCD in cyanobacteria under UV stress are not yet clear.

In addition to repairing DNA, cyanobacteria can replace damaged proteins by synthesizing new polypeptides in a multistep process called the "PSII repair cycle" [169]. The *de novo* synthesis of the D1 and D2 proteins of PSII is an important defense mechanism against the detrimental effects of UV-B radiation. The main step in this process is the differential transcription of the *psbA2*/*psb-A3* and *psbD1*/*psb-D2* genes encoding identical D1 and D2 proteins, respectively [170]. In the cyanobacterium *Synechocystis* sp., an increased turnover of D1 and D2 proteins is responsible for UV-B resistance [171]. Upon UV-B exposure, *Synechococcus* sp. PCC 7942 rapidly alters the expression of a family of three *psbA* genes, *psbAI*, *psbAII*, and *psbAIII*, which encode PSII D1 proteins [172,173]. Increased levels of the transcripts of *psbA2* (2–3-fold), *psbA3* (20–30-fold), *psbD1* (1.5–2-fold), and *psbD2* (5–7-fold) were observed under UV-B stress in *Synechocystis* sp. PCC6803, indicating their roles in defense against UV-B damage [170]. The expression of the *psbA* gene has recently been studied in several cyanobacteria, including *Thermosynechococcus elongatus* [174], *Gloeobacter violaceus* [175], and *Synechococcus* sp. [176]. Minda et al. provided genetic evidence of the role of the *psbA* gene family (encoding D1 proteins) in DNA repair/protection in *Synechocystis* sp. PCC 6803 [177]. Grasse et al. demonstrated that the Psb27 assembly factor is essential for the survival of cyanobacterial cells grown under stress conditions [178]. Wu et al. also confirmed that D1 protein turnover is involved in the protection of PSII from UV-B-induced damage in the cyanobacterium *Arthrospira* (*Spirulina*) *platensis* [47].

4. Conclusions

The increased incidence of UVR in the Earth's atmosphere with the release of anthropogenic ozone-depleting substances has generated tremendous concern about the harmful effects of UVR on terrestrial and aquatic ecosystems. Cyanobacteria, one of the most important producers of biomass, are susceptible to enhanced UVR stress, and a number of UV-induced effects have been reported in various cyanobacterial species. UV-B radiation can directly or indirectly damage cellular DNA, proteins, and physiological and biochemical processes through ROS-induced oxidative damage. Although ROS can regulate gene expression by acting as a second messenger in a variety of cellular signaling pathways that induce protective and adaptive responses [179], the precise role of ROS in signaling under UVR stress remains ambiguous in cyanobacteria. The adverse effects of UVR on this dominant microflora could disrupt the balance of entire ecosystems. However, in the course of evolution, cyanobacteria have developed cellular machinery and mechanisms to protect themselves, allowing them to survive and flourish in various sun-exposed environments under intense solar UVR. This has led to balanced and healthy ecosystems, in which environmental processes are maintained, including food web dynamics [180] and the biogeochemical cycles of nitrogen, carbon, and oxygen [181,182]. In response to UV-B radiation, several antioxidants, including SOD, CAT, and peroxidase, convert ROS into nontoxic products, eliminating superfluous free oxygen radicals. Antioxidants, including SOD and CAT, are found in several forms, but the expression of specific SODs and CATs in cyanobacteria under UVR remains unclear. EPS also play a significant role in the protection of cyanobacteria from DNA strand breaks and lipid peroxidation by efficiently eliminating the ROS induced by UV-B radiation [113]. EPS or exopolymers might also represent an effective means of transferring nutrients and metals through the lower marine food web [183]. However, information on the secretion and potential roles of EPS in many cyanobacteria is sparse, and the area warrants further research. An interesting property of cyanobacteria is their capacity to overcome UVR toxicity using UV-absorbing/screening compounds, such as MAAs and SCY. Some gene clusters involved in the biosynthesis of these compounds have recently been characterized, although research into the molecular biology and roles of MAAs and SCY is in its early stages. A number of efficient repair mechanisms, including photoreactivation, excision repair, and recombinational repair, can repair UV-induced DNA lesions in cyanobacteria. The SOS response and apoptosis (PCD) also contribute to stress tolerance in cyanobacteria [164,165]. Cyanobacterial filaments exposed to UVR can fragment after the PCD of severely damaged cells in the filament, although the degradation of the proteins that maintain these structures has been proposed to underlie filament breakage [13]. Therefore, it is unclear how PCD operates in cyanobacteria, and probing the similarities in PCD among cyanobacteria and animal, plant, and fungal models will be the aim of future research. Hsp expression is also assumed to be part of the endogenous response of cyanobacteria to UV, influencing DNA repair mechanisms and/or PCD induction [142]. Clarifying the occurrence and roles of Hsps in cyanobacteria under oxidative stress will require extensive research.

When extrapolating the results obtained from laboratory-based supplementary UV-B to the field, it should be borne in mind that the levels of UV-B radiation employed in laboratory studies may be unrealistically high and, furthermore, there may be no or inappropriate levels of UV-A. For example, in the mat-forming *P. murrayi* West and West, grown under white light combined with a range of UV-A and UV-B irradiances, growth inhibition depended upon the ratio of UV-B to UV-A, with growth rates increasing linearly with increasing levels of UV-A [184]. These results illustrate that the inhibitory effects of UV-B represent the balance between damage and repair processes that are controlled by distinct wavelengths of light and highlights the importance of ensuring that the UV spectral balance in laboratory and field experiments in UV-B toxicity are equivalent.

Although information about the diverse aspects of UV effects has accumulated in the last few decades, gaps remain that prevent a clear understanding of the UV tolerance mechanisms of cyanobacteria. However, overall, it seems that their dynamic stress tolerance mechanisms have allowed the cyanobacteria to become the most ecologically successful prokaryotes on Earth.

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