UV Stress Responses in Cyanobacteria

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Abstract

Cyanobacteria are the oldest group of prokaryotes with oxygen-evolving photosynthesis. They are supposed to have evolved in an atmosphere with little or no oxygen and therefore no protecting stratospheric ozone layer. Since cyanobacteria have to utilize sunlight for photosynthesis, they are simultaneously exposed to deleterious solar UV radiation. In order to survive, they had to develop countermeasures. One strategy is fast reproduction in order to make up for losses due to radiation damage. Another mechanism is mat and crust formation, which protects the organisms in lower levels while sacrificing the ones in the top layer. Vertical migration in the water column using changing buoyancy helps to bring the organisms out of the danger zone. Likewise, gliding cyanobacteria have been found to move to a position deeper in the water to avoid excessive UV exposure. Efficient repair mechanisms have been developed to replace damaged proteins in the photosynthetic apparatus and to repair damage in the cellular DNA. Many cyanobacteria synthesize UV-absorbing pigments such as mycosporine-like amino acids and scytonemin, deposited in the outer cell layers or extracellularly, which absorb UV photons before they can damage vital biomolecules within the cell.

Keywords

Cyanobacteria · UV stress · Repair mechanisms · UV-absorbing pigments · Migration · Buoyancy

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R. P. Rastogi (ed.), *Ecophysiology and Biochemistry of Cyanobacteria*,
https://doi.org/10.1007/978-981-16-4873-1_6

6.1 Introduction

Bacteria were the first organisms on earth using solar light to harvest energy. Most modern photosynthetic bacteria use a single photosystem (of two possible ones), which operates under anoxygenic conditions since oxygen is toxic to many prokaryotes. The active pigment is one of several bacteriochlorophylls. In contrast, cyanobacteria were the first organisms to develop oxygenic photosynthesis based on two photosystems, which operate in tandem. Oxygen is produced by splitting water. This process is thought to have started about 2.3 billion years ago and since then oxygen accumulates in the atmosphere (Soo et al. 2017). Cyanobacterial photosynthesis uses chlorophyll *a* in both reaction centers which eukaryotic plants also utilize; therefore, the latter are thought to have evolved from the prokaryotic ancestors, which have been taken up in the form of endosymbiosis (Cihlář et al. 2019).

Cyanobacteria can be unicellular, floating in fresh or marine water, or growing on terrestrial or underwater surfaces. While most have diameters of a few micrometers, some are so minute that they have long been overlooked in marine plankton communities because of the too large pore size of the common plankton nets. However, during the past few decades it was found that some of them, especially the picoplanktonic genera *Prochlorococcus* and *Synechococcus*, which are in the 0.1–1 μm diameter size class, form major components of the marine ecosystems (Casey et al. 2019). Assessments of the contribution of picoplankton to the total biomass in the top 150 m of the water column indicated that they may account for up to 50% or more with *Prochlorococcus* being the most abundant and responsible for 70% of the picoplankton population (Linacre et al. 2019). Figure 6.1 represents the morphological structure of some unicellular and filamentous cyanobacteria.

Unicellular cyanobacteria may form colonies, which are held together by the extracellular polysaccharide slime which the cells produce and excrete (Sato et al. 2017). *Microcystis* cells collected from Lake Mead, Nevada, USA, were found to produce an outer sheath up to 30 μm thick (He and Wert 2016). Other genera form unbranched, pseudo-branched, or truly branched uniseriate filaments, which are covered by a cylindrical slime tube (Kabirnataj et al. 2018; Singh 2017).

Cyanobacteria are found in almost all habitats on earth. Aquatic forms live both in fresh and marine waters. Terrestrial cyanobacteria are found from the tropics to polar regions; they can cover rocks, salt marshes and even the barks of trees. They are adapted to low temperatures and desiccation (Jimel 2020), while others can survive in hot thermal springs (Cheng et al. 2020). Several species of cyanobacteria have been reported from a hypersaline desert (Patel et al. 2019). A wide variety of cyanobacteria lives in symbioses with all kinds of plants and animals. Lichens are a symbiosis of algae and/or cyanobacteria with fungi (Pankratov et al. 2017), and the aquatic fern *Azolla* harbors cyanobacteria in thallus cavities (Sánchez-Baracaldo and Cardona 2020). Cyanobacteria have been found to form symbioses with diatoms, bryophytes, gymnosperms and angiosperms, and they are even found in symbiosis with animals such as marine sponges and worms (Rai 2018).

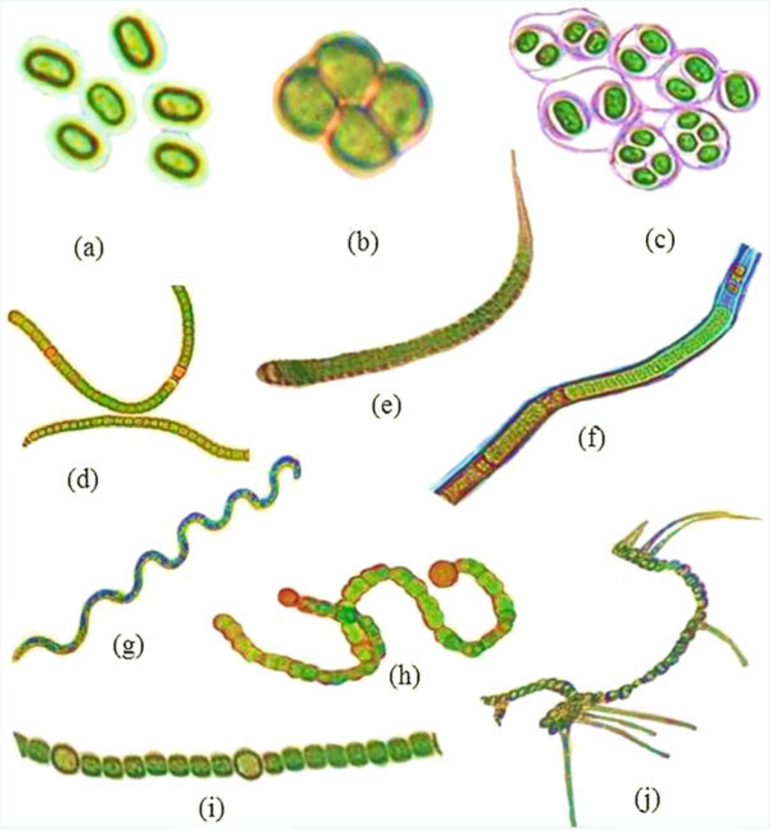

Fig. 6.1 Photographs showing the morphology of some cyanobacteria (**a**, *Gloeocapsa* sp.; **b**, *Chroococcus* sp.; **c**, *Cyanothece* sp.; **d**, *Scytonema* sp.; **e**, *Calothrix* sp.; **f**, *Lyngbya* sp.; **g**, *Arthrospira* sp.; **h**, *Nostoc* sp.; **i**, *Anabaena* sp.; **j**, *Fischerella* sp.). (Images by RP Rastogi)

In contrast to some earlier reports, cyanobacteria cannot swim in water (Menon et al. 2020). They do not have cilia, flagella or other moving organelles such as bacteria, flagellates and other eukaryotes (Miyata et al. 2020). But many are motile using a slow gliding movement. Some uniseriate filaments such as *Anabaena* or *Phormidium* glide within their sheath, which they may shed at the rear. They may also reverse their direction of movement triggered by external light or chemical stimuli. Motility has been studied in the model cyanobacterium *Synechocystis* sp., PCC 6803. In this organism, motility has been identified to be based on the presence of thick TFP pili, which can be extended, retracted and adhered to the substratum (Chen et al. 2020). Even though not capable of active swimming, planktonic cyanobacteria can undergo vertical migrations in the water column by changing their buoyancy (Kai and Lan 2020). This can be achieved by the production and collapse of gas vesicles (Dyer and Needoba 2020).

6.2 Exposure to Solar UV Radiation

Solar radiation can be subdivided into ultraviolet (UV, <400 nm), visible (400–700 nm), and infrared (IR, >700 nm). Infrared radiation can hardly be used for photosynthesis; however, there is one example of a cyanobacterium (*Synechococcus* PCC7335) which has a second core-membrane linker (ApcE2) of the phycobilisome which is noncovalently bound which allows the organism to utilize near IR (Miao et al. 2016).

The UV wavelength range can be subdivided into UV-C (<280 nm), UV-B (280–315 nm), and UV-A (315–400 nm) (Aphalo 2017). Photosynthesis is mainly supported by visible radiation, but under certain conditions (low radiation under cloud cover) UV-A can be utilized by some macroalgae (Xu and Gao 2016). Generally speaking, UV radiation is detrimental for organisms, especially at excessive intensities. Today, UV-C is quantitatively absorbed by oxygen and ozone in the atmosphere. UV-B is also significantly filtered out mainly by stratospheric ozone. But before the atmospheric oxygenation, organisms were exposed to and had to cope with much higher surface UV-B and in addition UV-C than today. This was the situation for cyanobacteria during their Achaean evolution even though the presence of Fe(III)-Si precipitates absorbed up to 70% of the incoming UV-C radiation. However, it is assumed that the remaining UV-C caused high mortality rates and limited cyanobacterial expansion in marine habitats (Mloszewska et al. 2018).

Solar irradiances strongly depend on a number of physical conditions on our planet. The solar zenith angle (SZA) determines the irradiance in all wavelength bands, which are highest in the tropics and gradually decrease toward the poles as monitored by 17 stations of the Eldonet network (Table 6.1). Much higher irradiances have been measured during a recent 1-year campaign in the high Andes near Laguna Lejia (Chile, latitude 23° 26′ 23.30″ S, longitude 67° 38′ 14.29″ W) at an elevation of 4715 m (Häder and Cabrol 2020). Figure 6.2 shows the mean monthly irradiances of PAR, UV-A, UV-B, and short-wavelength UV-B (295–310 nm).

Since today solar UV-C radiation does not hit the surface of the earth, UV-B is the most detrimental wavelength band for organisms exposed to solar radiation. In addition to latitude, UV-B radiation at ground level is controlled by the atmospheric water content (especially clouds), albedo and aerosols, and total column ozone (Häder and Cabrol 2020). At the same latitude, irradiances in the Southern Hemisphere are higher than in the Northern Hemisphere, because of the different earth–sun distances (Cordero et al. 2014). The stratospheric ozone concentration is lower in the tropics than at mid- and higher latitudes, resulting in higher solar UV-B irradiances. UV radiation increases with elevation (Blumthaler et al. 1997). In Northern Chile, IR increases by 27%, PAR by 6%, and UV by 20% from sea level to 5100 m altitude (Cordero et al. 2016). Clouds can reduce or enhance solar irradiation by absorption or scattering, quantified by the cloud modification factor (CMF) (Feister et al. 2015).

Stratospheric ozone depletion by chlorofluorocarbons (CFCs) and other anthropogenic trace gases such as organobromides and chlorocarbons has increased

Table 6.1 Location, latitude, longitude, elevation above sea level, and mean summer irradiances in PAR, UV-A, and UV-B measured by 17 ELDONET stations (after Häder et al. 2007)

Location	Latitude	Longitude	Elevation m a.s.l.	Summer irradiances [W m^{-2}] PAR ± S.D.	UV-A ± S.D.	UV-B ± S.D.
Abisko	68° 50′ N	19° 00′ E	385	284.69 ± 34.13	33.99 ± 9.05	0.77 ± 0.32
Lund	55° 07′ N	13° 04′ E	50	380.78 ± 32.52	59.92 ± 7.26	1.55 ± 0.47
Helgoland	54° 10′ N	07° 51′ E	61	353.11 ± 54.24	44.08 ± 6.32	0.77 ± 0.34
Erlangen	49° 35′ N	11° 00′ E	280	393.30 ± 35.40	52.70 ± 9.38	1.33 ± 0.30
Karlsruhe	49° 03′ N	08° 23′ E	200	385.14 ± 12.21	49.55 ± 7.14	1.07 ± 0.49
Ljubljana	46° 04′ N	14° 33′ E	300	412.84 ± 27.13	59.97 ± 2.89	1.52 ± 0.15
Bonassola	44° 10′ N	09° 30′ E	10	411.60 ± 37.38	61.23 ± 8.89	1.60 ± 0.29
Pisa	43° 43′ N	10° 23′ E	100	390.28 ± 0.08	55.46 ± 0.61	1.05 ± 0.03
Logrono	42° 28′ N	02° 27′ W	380	387.44 ± 26.45	57.48 ± 5.23	1.53 ± 0.21
Lisbon	38° 42′ N	09° 10′ W	105	398.67 ± 31.68	62.08 ± 8.55	1.60 ± 0.41
Athens	37° 58′ N	23° 46′ E	110	393.82 ± 49.42	55.91 ± 8.03	1.67 ± 0.85
Sierra Nevada	37° 04′ N	03° 20′ W	2850	430.87 ± 25.89	61.52 ± 3.76	1.88 ± 0.32
Malaga	36° 43′ N	04° 23′ W	18	414.21 ± 13.32	61.88 ± 2.96	1.90 ± 0.25
Gran Canaria	27° 55′ N	15° 35′ W	8	419.84 ± 20.31	64.26 ± 5.32	2.05 ± 0.24
Joinville	26° 15′ S	48° 55′ W	120	413.81 ± 0.19	55.31 ± 4.77	1.41 ± 0.36
Playa Union	43° 15′ S	65° 00′ W	20	424.26 ± 46.71	62.33 ± 3.68	1.89 ± 0.15
Lauder	45° 01′ S	169° 41′ E	370	429.08 ± 27.43	61.31 ± 5.23	1.70 ± 0.30

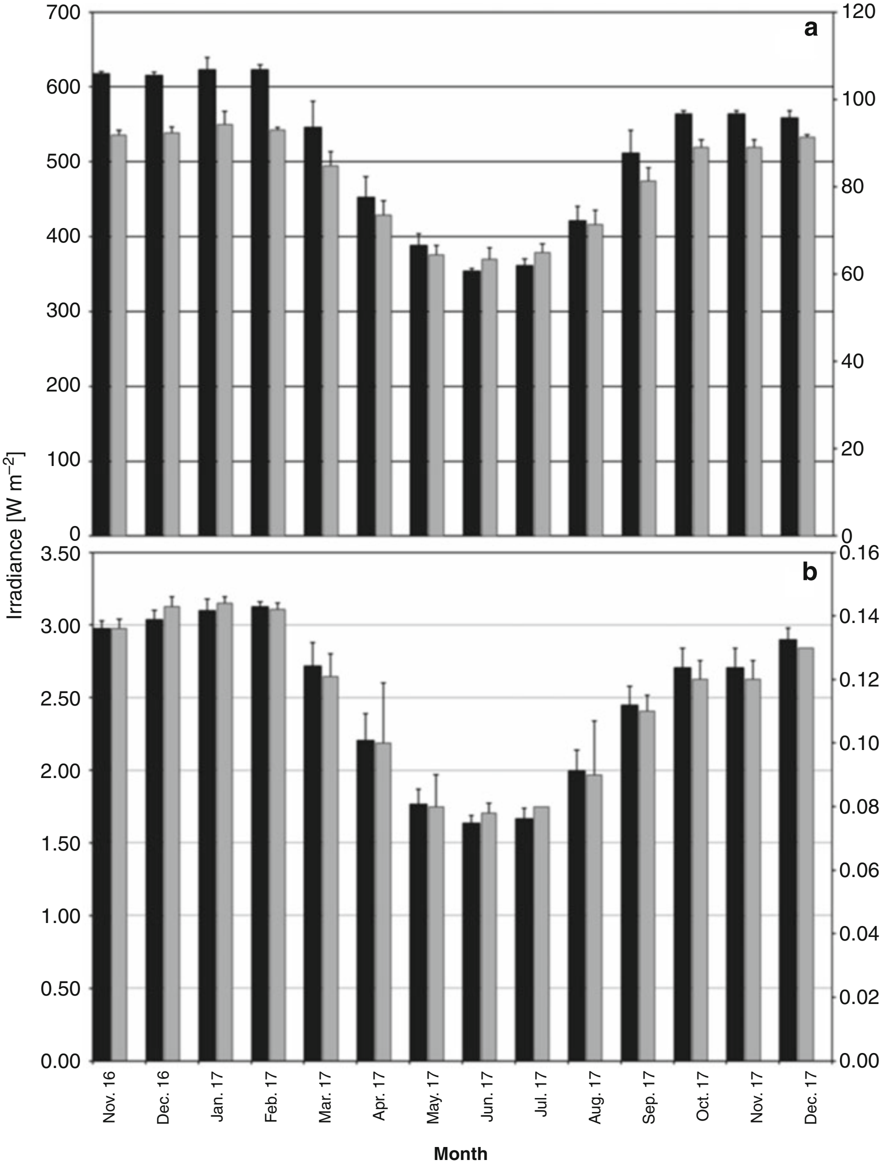

Fig. 6.2 Mean monthly irradiances of PAR, UV-A, UV-B, and short-wavelength UV-B (295–310 nm) monitored over a year in the high Andes (Laguna Lejia, Chile, latitude 23° 26′ 23.30″ S, longitude 67° 38′ 14.29″ W at an elevation of 4715 m) (Häder and Cabrol 2020)

terrestrial UV-B radiation, but due to the Montreal Protocol and its amendments this effect is stopped and slowly reverses (Bais et al. 2018). But a recovery to pre-1980 levels is predicted only for or after mid-century due to the long lifetimes of CFCs in the stratosphere, which can be decades (Hoffmann et al. 2014). Global climate change alters total column ozone and therefore UV irradiances (Williamson et al. 2014; Schnell et al. 2016; Meul et al. 2016).

6.3 UV Effects on Cyanobacteria

There are a several nonphotosynthetic cyanobacteria whose diversity, distribution, and ecology are currently hardly known (Monchamp et al. 2019). Some are found in dark, deep terrestrial habitats such as rocks using a hydrogen-based lithoautotrophic metabolism (Puente-Sánchez et al. 2018). In contrast, all photosynthetic cyanobacteria require solar radiation for their energy harvesting. Therefore, they are inevitably exposed to solar UV radiation. Solar UV radiation affects several key cellular biomolecules and machinery (e.g., DNA and proteins), cellular morphology, photosynthesis, growth, survival, pigmentation, and nitrogen metabolism enzymes in cyanobacteria (Sinha et al. 1995a, 1998; Kumar et al. 1996; Rastogi et al. 2014a, b).

6.3.1 Damage and Repair of DNA

The most deleterious UV-B radiation is absorbed by important biomolecules including proteins, nucleic acids, and lipids, resulting in considerable damage of exposed organisms and affecting physiological, biochemical, and ecological functions, such as morphology, differentiation, growth, development, pigmentation, and motility and orientation (Häder 1993a, b; Pathak et al. 2018). Absorption of UV-B photons by the cellular DNA results in the formation of cyclobutane pyrimidine dimers (CPDs), which are the most notable lesions (about 75–80%) induced by solar UV radiations (Pathak et al. 2019b; Rastogi et al. 2010a) (Fig. 6.3). Besides CPDs, 6-4 photoproducts (6-4PPs), are the second most frequently occurring DNA lesions (about 20–25%), which are formed mainly under UV-C and readily converted into their Dewar valence isomers upon exposure to UV radiation (Rastogi et al. 2010a) (Fig. 6.4).

These dimers are induced between two adjacent pyrimidine bases (thymine, cytosine, and uracil). This defect seems like a minor change in the structure of the DNA, but may have far-reaching consequences for the biochemical processes in the cell since the DNA reproduction and transcription into RNA are stopped there.

CPDs are repaired by the cells in a process called photoreactivation, which involves the enzyme DNA photolyase (Rastogi et al. 2011). This enzyme possesses two noncovalently linked cofactors such as $FADH_2$ and absorbs blue or UV-A photons and uses their energy to split the dimer (Pathak et al. 2019b; Rastogi et al. 2020). If the lesion is not repaired, it results in s signature mutation (Brash and Seidman 2020). Photolyases are very old enzymes found in bacteria all the way to vertebrates (Sinha and Häder 2002; Zhang et al. 2013). In cyanobacteria, this process has been studied, e.g., in *Anacystis nidulans*, and the enzyme has been purified (Eker

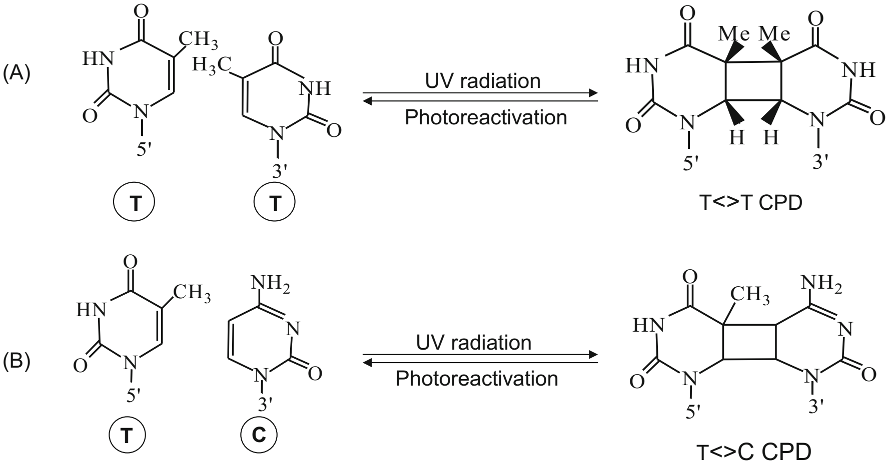

Fig. 6.3 Formation of cyclobutane–pyrimidine dimers (CPDs) induced mainly by UV-B on DNA having adjacent thymine/cytosine bases. (**a**) Thymine–thymine cyclobutane–pyrimidine dimer (T<>T CPD) and (**b**) thymine–cytosine cyclobutane–pyrimidine (T<>C CPD) dimer. Both T<>T and T<>C CPDs split to form two canonical thymine/cytosine bases by means of photoreactivation in the presence of the photolyase enzyme (Rastogi et al. 2010a)

et al. 1990). However, it is interesting to note that placental mammals including humans lack this repair mechanism and must rely on other DNA repair mechanisms such as nucleotide excision repair (see below) (Jans et al. 2005). UV-C mainly induces the formation of thymine–pyrimidone (6-4) dimers. These lesions are also repaired by a photolyase (Kavakli et al. 2019).

Other UV-induced DNA damages include DNA–protein crosslinks (Rastogi 2010; Richa et al. 2015; Rajneesh et al. 2018) and 8-oxo-7,8-dihydroguanyl, 8-oxo-Ade, 2,6-diamino-4-hydroxy-5-formamidoguanine and oxazolone, which result from oxidations products of purine bases of the DNA (Doetsch et al. 1995; Hall et al. 1996).

DNA lesions, which are not repaired by a photolyase during photoreactivation, can be mended by excision repair (see review by Pathak et al. 2019b). This mechanism is independent of light and uses several enzymes (Bergi and Trivedi 2020). It is based on the removal of a small number of bases, e.g., after a single-strand break, which are subsequently resynthesized and inserted using the complementary strand. One form of excision repair is the base excision repair pathway in which one or two bases are removed and substituted after, e.g., desiccation or radiation stress (Singh 2018). The alternative is nucleotide excision repair, which removes DNA lesions including CPDs or 6,4 photoproducts (6,4 PPs), DNA intrastrand crosslinks, chemical adducts, or by oxidative damage by reactive oxygen species (Sinha 2017).

Recombinational repair is a powerful mechanism to restore the correct DNA sequence after single- or double-strand DNA breaks. This pathway is fairly complex involving more than 20 gene products in *E. coli*. Initially, an exonuclease enlarges

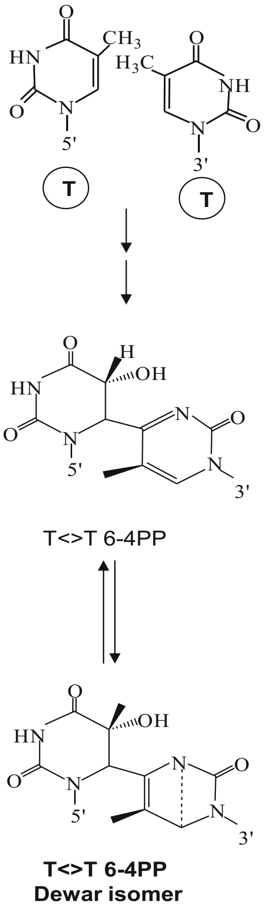

Fig. 6.4 Formation of DNA lesion 6-4 photoproducts (6-4PPs) and their Dewar valence isomers (Rastogi et al. 2010a)

the DNA break and the gap is identified by RecFOR proteins. Subsequently, RecBCD and RecFOR perform the repair by homologous recombination (Rastogi et al. 2015). If all fails, cells retreat to the last resort, called SOS repair. This is initiated by different and substantial DNA damages or when the DNA replication is inhibited as studied in the cyanobacterium *Anabaena* sp. (Kumar et al. 2018). This pathway relies on the interaction of several repressor proteins including RecA and LexA, which block the 40 or so SOS response genes. Once the blockage is released, the SOS genes, each consisting of a 20-nucleotide-long SOS box, start their work. One of them codes for the SulA protein, which delays the cell division until all damages are repaired. However, many differences in the components of the SOS repair mechanism exist between bacteria and cyanobacteria and between species (Kumar et al. 2018).

6.3.2 Reactive Oxygen Species

Solar UV-B does not have to exert direct effects on cellular targets. It may be absorbed by proteins or other biomolecules in the cell upon which the excitation energy of the UV photon is transferred to, e.g., oxygen, which results in the formation of reactive oxygen species (ROS). The reduction of molecular oxygen results in superoxide, which may lead to the production of most other ROS (Turrens 2003).

$$O_2 + e^- \rightarrow {}^{\bullet}O_2{}^-$$

Dismutation of superoxide results in hydrogen peroxide

$$2H^+ + {}^{\bullet}O_2{}^- + {}^{\bullet}O_2{}^- \rightarrow H_2O_2 + O_2$$

which may be partially reduced to a hydroxide ion and a hydroxyl radical or may be fully reduced to water

$$H_2O_2 + e^- \rightarrow HO^- + {}^{\bullet}OH$$

$$2H^+ + 2e^- + H_2O_2 \rightarrow 2H_2O$$

Another pathway transfers the excited energy of an absorbing molecule, such as chlorophyll, to a nearby oxygen (the ground state of which is a triplet state, ${}^3O_2$) which is converted to singlet oxygen (${}^1O_2$) which is highly reactive and destructs nearby biomolecules and structures, even though its lifetime is rather short (on the order of 10–40 ns) (Moan and Berg 1991). In this case, the chlorophyll acts as a photosensitizer (Ph). This response is a major damaging mechanism in photosynthesis (Krieger-Liszkay 2005) but also occurs in mitochondria (Thomas et al. 1992). As an aside: This photodynamic reaction induced by introduced photosensitizers such as hematoporphyrin is used in medical treatment of superficial cancers in humans (Lv et al. 2016).

$$Ph + h\nu \rightarrow {}^3Ph$$

$${}^3Ph + {}^3O_2 \rightarrow Ph + {}^1O_2$$

Oxygen is toxic at higher concentrations. After the development of an oxygenic atmosphere on our planet, many early life forms such as bacteria had to find protection from the increasing oxygen concentration. Today, many of these bacteria are confined to anoxic environments such as sediments (Valentine 2002). All other organisms were forced by the environmental pressure to develop mechanisms to protect themselves from ROS. This is mainly achieved by two different mechanisms. One is the employment of passive antioxidants such as ascorbic acid, α-tocopherol, glutathione, lycopene, lutein, and isoflavones (Sindhi et al. 2013). Such ROS scavengers are also found in many cyanobacteria (Radyukina et al. 2019; He and

Häder 2002b). The alternative strategy to counter the stress of ROS is the involvement of antioxidant enzymes such as superoxide dismutase (SOD), catalase, glutathione peroxidase, ascorbate peroxidase, monodehydroascorbate reductase, dehydroascorbate reductase, or glutathione reductase found, e.g., in *Anabaena* sp. (He and Häder 2002a) and other cyanobacteria (Aráoz and Häder 1999a). The production of ROS induced by UV-B radiation can be shown and monitored by employing the ROS-sensitive, oxygen-sensing probe 2′,7-′-dichlorodihydrofluorescein diacetate (DCFH-DA) (He and Häder 2002a; Rastogi et al. 2010b).

6.4 UV Damage of the Photosynthetic Apparatus and Repair

The photosynthetic apparatus is a key target of damaging solar UV radiation. In addition to unspecific effects on proteins, lipids, membranes, and other biologically important molecules and structures, UV-B affects the photosynthetic electron transport, quantum yield, and oxygen production (Xue et al. 2005). Exposure to UV radiation bleaches the photosynthetic pigments in the cyanobacterium *Phormidium uncinatum* (Donkor and Häder 1997; Sinha et al. 2005). Phycobilisomes containing the phycobiliprotein accessory pigments are broken down into smaller components by increasing exposure (Sinha et al. 1995c, b). In the initial phase of exposure, the phycobiliprotein fluorescence increases indicating that they can no longer transfer the excitation energy to the photosynthetic reaction centers (Donkor and Häder 1996). After prolonged exposure to UV, the fluorescence of the accessory phycobiliproteins decreases (Rastogi et al. 2015). Photodegradation of phycobilisomes by UV radiation was also confirmed in *Nostoc* sp. and *Aulosira fertilissima* (Aráoz García 1998; Banerjee et al. 1998). Exposure to UV radiation also impairs the translation activity in the cyanobacterium *Nostoc* sp. (Araoz et al. 1998). In contrast, low-level UV-B irradiances induce phycoerythrin synthesis in *Nostoc* (Aráoz and Häder 1999b).

As indicated above, ROS generated by photodynamic reactions are a potential mechanism to damage biomolecules and structures within the photosynthetic apparatus. Solar energy is absorbed by accessory pigments such as phycobilins in the phycobilisomes of cyanobacteria (as well as by chlorophyll *b*, chlorophyll *c,* or chlorophyll *d* in algae and higher plants) and transferred to the photosynthetic reaction centers of photosystems I and II (Jaiswal et al. 2018). An excited electron from the special chlorophyll *a* dimer P680 in PS II is transferred to a primary acceptor (pheophytin) (Khaing et al. 2019) from where it is handed along a chain of redox components via P700, the reaction center PS I (where the electron is again excited to a higher energetic level) until it is finally utilized to reduce NADP (Tikhonov and Subczynski 2019). The missing electron in P680 is subsequently replaced by an electron generated by the photolytic splitting of water on the inside of the thylakoids by an enzymatic Mn complex (Böhmer et al. 2017).

$$H_2O \rightarrow ½O_2 + 2H^+ + 2e^-$$

The oxygen is released as a waste product and the protons are used to drive an ATPase, which generates ATP, which is used together with the reduction equivalents (reduced NADP) to reduce CO_2 to sugar in the Calvin cycle (Michelet et al. 2013; Janasch et al. 2019). Under high light conditions, the electron transport chain is fully reduced and cannot accept any more electrons from P680 (Lea-Smith et al. 2016). Therefore, the excitation energy can be transferred to a nearby oxygen resulting in singlet oxygen (s. above) (Lee and Min 2010). In order to avoid this, potential damaging situation-specific carotenoids are arranged in close vicinity to the chlorophyll so that the excitation energy can be transferred to the carotenoids, which relax the energy in the form of heat (Pospíšil and Prasad 2014; Schäfer et al. 2005).

Another target of solar UV is the D1 protein located in PS II encoded by the *psbAI* gene (Rexroth et al. 2017). This protein is responsible to transfer the excited electrons from P680 to pheophytin (Khaing et al. 2019). This protein is easily kinked by excessive visible or UV radiation, which stops the electron transport. This lesion is rapidly repaired by proteolytic removal of the damaged protein and subsequent replacement by a newly synthesized protein (Campbell et al. 1998; Ehling-Schulz and Scherer 1999).

6.5 Motility and Orientation

As indicated above, many unicellular and multicellular cyanobacteria are motile. Some show a gliding motility, others use changes in buoyancy to realize vertical migration. These mechanisms are used to avoid areas of deleterious solar radiation. Picoplanktons, such as *Synechococcus* and *Prochlorococcus*, which are major biomass producers in the oceans, use fast reproduction to overcome the population losses due to excessive UV (Häder and Gao 2018). In addition, there is a pronounced seasonal variability and changes in vertical distribution (Al-Otaibi et al. 2020). In the Red Sea, *Synechococcus* was found close to the surface, while *Prochlorococcus* was responsible for a chlorophyll maximum between 40 and 76 m. *Prochlorococcus* populations had a maximum in summer and a minimum in winter, while *Synechococcus* showed the opposite temporal distribution. In addition, there are low light- and high light adapted genetically different populations dwelling at different depths (Linacre et al. 2019).

Cyanobacteria with gliding motility respond to visible and UV radiation to select a suitable habitat. The coccoid *Synechocystis* sp. secretes a mixture of complex polysaccharides to drive their motility (Varuni et al. 2017) and shows a pronounced phototaxis, which can be positive (toward the light source) at low irradiances or negative (away from the light source) at high irradiances, while the rod-shaped *Synechococcus elongatus* PCC 7942 has no phototactic motility (Yang et al. 2018). In *Synechocystis* sp., PCC6803 a blue light-dependent signal cascade controls positive and negative phototaxis (Sugimoto et al. 2017). The cyanobacterial phytochrome 2 regulates the expression of motility-related genes via the second messenger cyclic-GMP (Wallner et al. 2020).

Also, some filamentous cyanobacteria show a gliding motility when in contact with a surface (Qiu et al. 2019). While the exact mechanism has not yet been revealed, several distinct structural features such as specifically arranged protein fibrils and organelle-like structures have been identified, which are thought to be involved in the secretion of mucilage (Hoiczyk 2000). The unbranched heterotrichous *Anabaena variabilis* has been found to move either as straight filaments or in a U-shaped form (Nultsch and Wenderoth 1983; Nultsch et al. 1979). When irradiated, the trichomes bend toward the light at low fluence rates (1.35 W m^{-2}) and away from the light source at higher (27 W m^{-2}). These authors assumed that the switch from positive to negative phototaxis is controlled by the intracellular level of singlet oxygen since gassing the moving filaments with N_2 or Ar shifts the transition from positive to negative phototaxis to higher irradiances (Nultsch and Schuchart 1985). The photoreceptor for photoorientation is assumed to consist of a superfamily of tetrapyrrole-binding molecules, cyanobacteriochromes (Ikeuchi and Ishizuka 2008). Exposure to UV-B radiation delays differentiation of vegetative cells into heterocysts and akinetes (Blakefield and Harris 1994), induces bleaching of the phycobilins (Agel et al. 1987), and affects productivity and nitrogen fixation in *Anabaena* (Lesser 2008). It also causes a significant decrease in the quantum yield of PSII. The effects on photosynthesis are thought to be due to the production of ROS, since exposure to UVR results in an increase in the level of superoxide dismutase.

The nonheterocystous filamentous *Phormidium uncinatum* does not show phototaxis, but orients with respect to light using photophobic responses. When a trichome enters a bright light field from a dark area, e.g., when it leaves the shade under a leaf, it reverses the direction of movement and glides back; this response is called a step-up photophobic reaction. In contrast, when leaving a low irradiance area moving into a dark area, it may also reverse the direction of movement (step-down photophobic response) (Nultsch and Häder 1970). The organisms respond even to small differences in the irradiances of two adjacent light fields as low as 4%. This can be demonstrated by projecting a photographic negative onto a population of *Phormidium* trichomes, which accumulate in areas of appropriate irradiance, forming a photographic positive (Häder 1984) (Fig. 6.5). The photosynthetic pigments are responsible for the photophobic responses in this cyanobacterium (Nultsch and Häder 1974; Häder 1974). The direction of movement is controlled by an electric potential gradient along the length of the trichome. During a photophobic reversal of movement, this gradient inverts (Häder 1978; Häder and Burkart 1978).

Motility of *Phormidium* is strongly impaired by solar and monochromatic UV irradiation (Häder et al. 1986). The action spectrum shows a strong response in the UV-B. In contrast, the photophobic response was not impaired by solar or artificial UV radiation (Häder and Häder 1990). Bleaching kinetics indicate that the accessory phycobilins, D-phycoerythrin, is easily bleached by UV radiation, followed by the

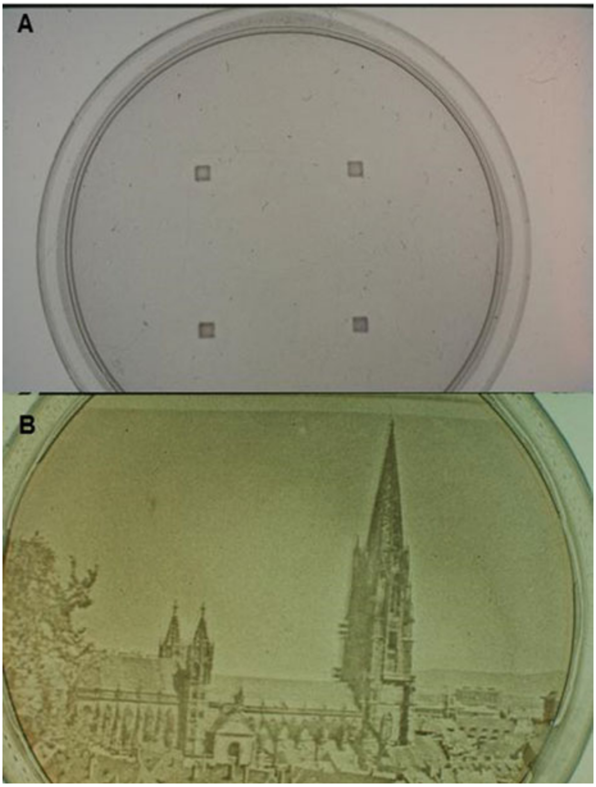

Fig. 6.5 *Phormidium* trichomes accumulate in low irradiance light fields projected onto a Petri dish (**A**). A photographic negative of the Münster in Freiburg has been projected onto a suspension of *Phormidium* trichomes, which accumulate in areas of appropriate irradiances forming a photographic positive (**B**) (after (Häder 1984))

carotenoids, while chlorophyll *a* was found to be the most resistant pigment to bleaching.

Several filamentous cyanobacteria (*Phormidium uncinatum*, two strains, *Anabaena variabilis and Oscillatoria tenuis*) protect themselves by vertical migration. The filaments were suspended in an agar layer inside a slanting groove made from dark PVC, which was placed in a pond reaching from 10 to 100 cm. After 4-h exposure to solar radiation, the organisms had moved to a position at about 50–60 cm below the water surface (Donkor and Häder 1995). Mat-forming *Oscillatoria* on Antarctica's McMurdo Ice Shelf have also been found to show vertical migration controlled by solar visible and UV radiation: At low irradiances (<8 W m^{-2}, no UV), the filaments migrated completely to the surface, while higher irradiances (>60 W m^{-2}, including UV-A and UV-B) induced downward migration (Nadeau et al. 1999). Similar vertical migrations were also found in *Microcoleus* and *Halomicronema* in microbial mats in the French Camargue (Fourçans et al. 2006) and in coastal microbial mats (Lichtenberg et al. 2020).

6.6 UV-Screening Pigments

In response to the pressure of solar UV radiation, many cyanobacteria (but also eukaryotic phytoplankton and macroalgae) have developed UV-absorbing pigments such as mycosporine-like amino acids (MAAs) and scytonemin (Scy) to screen out deleterious radiation before it can hit essential biomolecules and cellular structures (Sinha et al. 2007). Picoplanktons, such as the marine *Synechococcus* and *Prochlorococcus*, are too small (<1 μm) to use UV-screening pigments since the concentration would have to be too high to be effective over very small transmission distances (Garcia-Pichel 1994); therefore, these organisms rely on vertical migration, repair mechanisms, and fast replication to counter the challenge of solar UV radiation.

Mycosporine-like amino acids (MAAs) are small, hydrophilic, and colorless molecules with a cyclohexenimine or cyclohexenone chromophore attached to the nitrogen substituent of an amino acid or its imino alcohol (Pathak et al. 2019a). More than 20 different MAAs are known today, which are characterized by their high molar extinction coefficients (28,100–50,000 $M^{-1}\ cm^{-1}$) and a strong absorption in the UV between 310 and 362 nm (Pathak et al. 2017a; Rastogi et al. 2020) (Fig. 6.6). The absorbed UV photon energy is dissipated as heat and does not result in ROS generation (Conde et al. 2007). Some MAAs have even be found to possess free radical scavenging capacity (Rastogi et al. 2016).

Some cyanobacteria—and only this group of organisms—have developed another group of UV-absorbing pigments, i.e., scytonemins (Rastogi et al. 2012, 2014c). These molecules are heterocyclic phenolic dimers, which are excreted into the extracellular polysaccharide sheath (Pathak et al. 2017a, b) (Fig. 6.7). In addition to a major peak at 386 nm, the oxidized form shows peaks at 252 and 300 nm. The UV-C peak may be a reminder of the life history of cyanobacteria in an anoxygenic atmosphere with no stratospheric ozone layer. In *Nostoc punctiforme,* the molecule is coded by a gene cluster of 18 ORFs (Soule et al. 2007), and a possible biosynthesis pathway has been suggested by Balskus and Walsh (2009).

6.7 Conclusions

Photosynthetic organisms require solar energy for their metabolism. Simultaneously, they are exposed to deleterious UV-A and UV-B radiation, since cyanobacteria have started their development on our planet when the atmosphere contained only traces of oxygen, and consequently, no stratospheric ozone layer existed to protect them from the even more energetic UV-C radiation. At moderate irradiances, UV-A can be utilized to drive photosynthesis in some phytoplankton, but shorter wavelengths are always detrimental for living organisms. UV photons are absorbed by lipids, proteins, and other biologically important molecules and are consequently prone to modify these components and destroy cellular structures. In addition, absorption of solar UV radiation can induce reactive oxygen species (ROS).

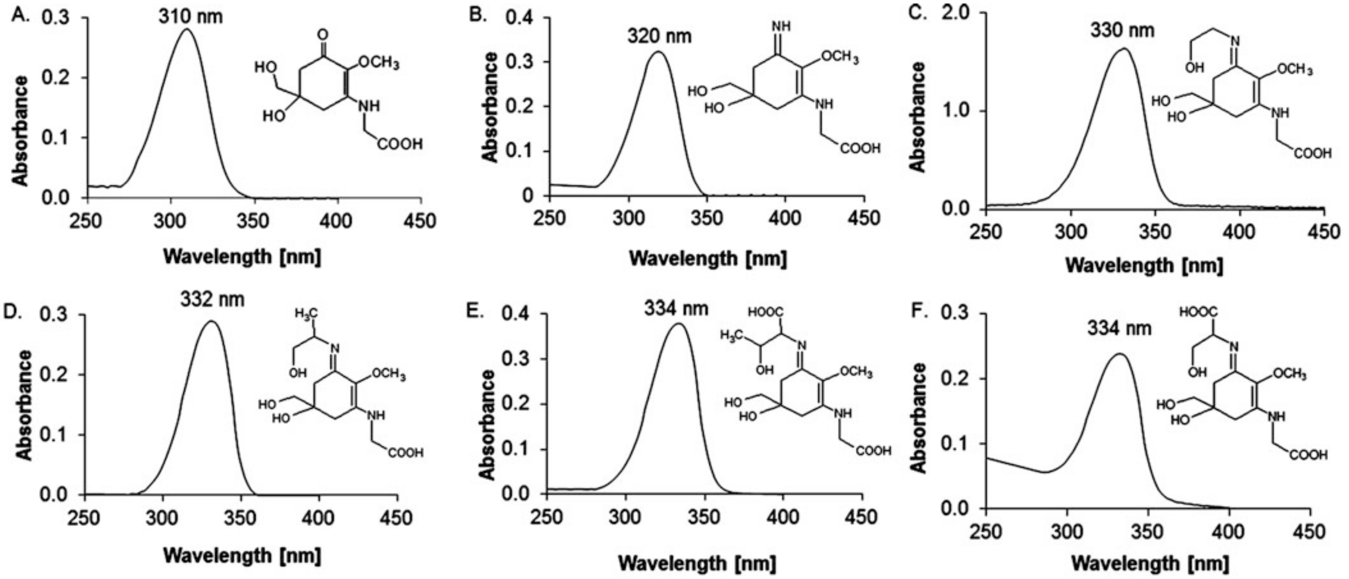

Fig. 6.6 Chemical structure of some common MAAs and their absorption spectra reported in different cyanobacteria. (**a**) M-Glycine; (**b**) palythine; (**c**) asterina; (**d**) palythinol; (**e**) porphyra-334; and (**f**) shinorine

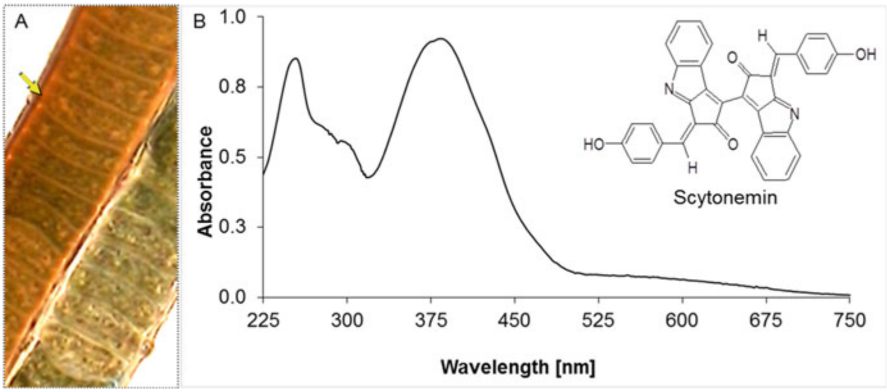

Fig. 6.7 Occurrence of scytonemin in the extracellular sheath (shown by arrow) of *Lyngby* sp. (**a**), their chemical structure and UV absorption maxima (**b**)

In order to protect the cells from deleterious solar UV radiation, organisms have developed a plethora of mechanisms and strategies against induced damage. The DNA is a key target of solar UV-B radiation, which is of vital importance since its integrity warrants the correct transmission of information to the next generation. Therefore, a large number of concepts have been developed to repair any UV-induced damage and modification including the involvement of photolyases, which remove dimers in the nucleotide strand. Other mechanisms include excision, recombination, and SOS repair pathways. A likewise important target of solar UV radiation is the photosynthetic apparatus. Short-wavelength photons bleach accessory pigments and chlorophyll *a* and induce ROS such as singlet oxygen, which in turn destroys biologically important structures. Cells have developed enzymatic and nonenzymatic strategies to quench ROS production. Damage of the redox elements of the photosynthetic electron transport chain is repaired by removal of mutilated proteins and replacement by newly synthesized molecules.

Other strategies to avoid excessive exposure to solar radiation include mat formation and vertical migration to bring organisms out of the danger zone. This can be achieved by using phototaxis or photophobic responses. One important mechanism is the production and incorporation of UV-absorbing pigments such as mycosporine-like amino acids and scytonemins, which prevent the transmission of damaging photons to vital biomolecules and structures in the center of the cell. In addition, some of these substances have antioxidant properties. These molecules have a potential to serve humans as UV protectants in suntan lotions as a replacement of artificial organic molecules (Guillerme et al. 2017; Richa and Sinha 2013).

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