

Chapter 1

Introduction

1.1 Origin of Cyanobacteria and Evolution of Life

Cyanobacteria are gram-negative oxygenic photosynthetic organisms. Although invisible to the naked eye, cyanobacteria are an essential component of the earth's biota. They catalyze unique and requisite transformations in the biogeochemical cycles of the biosphere, produce oxygen, an important component of the earth's atmosphere, and stand for a large portion of life's genetic diversity. Iron, the key metal of the universe played an important part in the origin of cyanobacteria and further evolution of life. Iron 60 provides the evidence in favor of a supernova explosion being the trigger for the formation of the solar system. The survival of life on the planet is feasible due to the liquid iron of the earth's core that created the magnetic field, without which the early atmosphere would have been stripped away and life could never have evolved. Fe^{2+} -mediated RNA folding and catalysis, in combination with the paleogeological models, suggest that RNA functioned and evolved in association with Fe^{2+} . Evidence also shows that the photochemical redox-cycling of $\text{Fe}^{2+}/\text{Fe}^{3+}$ could have provided the necessary high energy, reducing equivalents for the formation of H_2 , CH_4 , and other important ingredients for the assembly of amino acids in this abiotic world (Braterman et al. 1983; Huber and Wächtershäuser 1997).

Life on earth originated at least 3500 Ma and the principal mode of metabolism is thought to have been anaerobic fermentation of organic compounds, which had formed, abiologically in the primeval environment (Lemmon 1970). The ferredoxins (iron-sulfur protein) probably played a significant role in the development of fermentative bacteria. It is generally considered (Schilling 1973) that sulfur reduction was one of the earliest forms of microbial respiration, because the known microorganisms that are most closely related to the last common ancestor of modern life are primarily anaerobic, sulfur-reducing hyper thermophiles (White et al. 1995). However, geochemical evidence indicates that Fe (III) is more likely than sulfur to have been the first external electron acceptor of global significance in microbial metabolism (Rich and McKenzie 1981). Archaea and bacteria that are most closely related to the last common ancestor can reduce Fe (III) to Fe (II) and conserve energy to support growth.

The most widespread source of reducing power in late Archean and early Proterozoic (2.9–1.6 Ga) seawater was ferrous iron (0.1–1.0 mM) (Walker 1983), and several authors (Pierson and Olson 1989) proposed that ferrous iron might have been an early electron donor to PS II. The common ancestor of proteobacteria and cyanobacteria might well have used $\text{Fe}(\text{OH})^+$ as the principal electron donor for CO_2 fixation (Heising and Schink 1998). Although there is still considerable controversy about the exact time the cyanobacteria started to appear on Earth, there is no doubt that they are extremely ancient organisms. Before oxygen evolution by water splitting, cyanobacteria might well have used $\text{Fe}(\text{OH})^+$ as the principal electron donor for CO_2 fixation than other anoxygenic phototrophs. However, the photosystem I (PS I), photosystem II (PS II), and the oxygen evolving complex (OEC) in cyanobacteria appears to have been driven by the necessity to replace $\text{Fe}(\text{OH})^+$ with water as an electron donor to fix CO_2 most efficiently in the absence of ferrous iron and leads to evolution of oxygen. Olson 2001 proposed that the driving force for the evolution of PS-II in addition to PS-I was the necessity to utilize $\text{Fe}(\text{OH})^+$ effectively for CO_2 fixation in the absence of reduced sulfur compounds. This entailed the evolution of a water-splitting enzyme and the addition of a second photosystem, acting in series with the first, to bridge the enormous gap in redox potential between H_2O and NADPH. The present-day structural homologies between photosystems suggest that this change involved the cooperation of a photosystem derived from green bacteria (photosystem I) with a photosystem derived from purple bacteria (photosystem II). The biological consequences of this evolutionary step were far-reaching. For the first time, these cyanobacteria were able to survive with only very minimal chemical demands of their environment. These cells could spread and evolve in ways denied to the earlier photosynthetic bacteria, which needed H_2S or organic acids as a source of electrons. Consequently, large amounts of biologically synthesized, reduced organic materials accumulated. The increase in atmospheric O_2 was very slow at first and would have allowed a gradual evolution of protective devices. The early seas contained large amounts of iron in its ferrous oxidation state (Fe^{2+}), and nearly all the O_2 produced by early photosynthetic cyanobacteria was utilized in converting Fe^{2+} to Fe^{3+} . This conversion caused the precipitation of huge amounts of ferric oxides, and the extensive banded iron formations in sedimentary rocks beginning about 2.7×10^9 years ago. By about 2×10^9 years ago, the supply of ferrous iron was exhausted, and the deposition of further iron precipitates ceased and moreover, oxygen entered the atmosphere for the first time. Geological evidence suggests that O_2 levels in the atmosphere then began to rise, reaching current levels between 0.5 and 1.5×10^9 years ago. Therefore, this phenomena of evolution of oxygen remarkable shift in biology that required transformations in biochemical mechanisms and metabolic pathways permitted the evolution of new life-forms in which cyanobacteria play a major role. Much of the internal structure and biochemistry of plastids of higher plants, for instance the presence of thylakoids and particular chlorophylls, is very similar to that of cyanobacteria. According to the endosymbiotic theory, the chloroplasts found in plants and eukaryotic algae evolved from cyanobacterial ancestors via endosymbiosis and the phylogenetic estimates constructed with bacteria, plastids, and eukaryotic genomes also suggest that plastids are most closely related to cyanobacteria. So, cyanobacteria are the key to the evolution of life in this earth.

1.2 Extreme Environments Inhabited by Cyanobacteria and Their Diversity

Cyanobacteria are one of the most successful groups of organisms this planet has ever seen, and include some of the first life forms to evolve on Earth. During their long evolutionary history, cyanobacteria have undergone several structural and functional modifications, and these are responsible for their versatile physiology and wide ecological tolerance. They had to adapt various environmental conditions, from almost anoxic to present oxygen-rich atmosphere, to varying average temperature of the planetary surface, to changes in intensity and spectral composition of light resulting from the changes in composition of the atmosphere and to changes associated with movement to other biotopes. During this process cyanobacteria come up as one of the extremophilic organism. Cyanobacteria occupy almost all the environments on the earth that are illuminated with visible light. Among these habitats there are several places, which are from the anthropocentric view, inhospitable and different from the “normal” places. Extremophiles are classified into various categories according to the “extreme” character of their environments, such as very high or very low temperature limit, pH values, salinity, dryness, high concentration of heavy metals, very high or low levels of radiation, especially ultraviolet radiation, and to a certain extent anaerobic environments. Cyanobacteria are very well equipped to live under extreme environmental conditions such as hyper saline, alkaline, high or low temperature, desiccation, highlight, UV, etc. Contrary to the general belief, many cyanobacteria are not generalists. Many species appear to be highly specialized organisms and can adapt themselves to a narrow set of environmental conditions, particularly in the case of extreme environments. However, our knowledge about the nature of their adaptations is fragmentary. The success of cyanobacteria is not exclusively found in their metabolic diversity, flexibility, and reactivity and they can be diverse and evolve rapidly when conditions change. The diversity of cyanobacteria in various extreme habitats is summarized as follows.

1.2.1 *Thermophilic Cyanobacteria*

Many geothermal springs emit water near the boiling point. The gradual cooling of the water in the outflow channels provides a stable temperature gradient in which many cyanobacteria position themselves according to their temperature requirements. It is established that 73–74 °C is the maximum temperature enabling development of cyanobacteria. The existence of thermophilic cyanobacteria has been extensively documented in the course of the microbiological characterization of hot springs, first in Yellowstone National Park, Wyoming, USA (Brock 1969, 1978) and later in other geothermal areas all over the world (Castenholz 1969; Sompong et al. 2005). Different types of unicellular cyanobacteria, classified in the genus *Synechococcus* (*Thermosynechococcus*), are the most thermophilic. There are distinct differences in the communities found in hot springs in different parts of the

world. Thermophilic *Synechococcus* species, abundant in Yellowstone, are absent in similar hot springs in Iceland (Ward and Castenholz 2000). Filamentous cyanobacteria are less thermo-tolerant *Mastigocladus laminosus*, *Phormidium* sp., and different thermophilic *Oscillatoria* species have their upper temperature limit for growth between 55 and 62 °C where as *Chlorogloeopsis* have the upper temperature limit 65 °C.

1.2.2 Psychrophilic Cyanobacteria

Information on the life of cyanobacteria near the freezing point of water was collected in the Antarctic (Vincent 2000). A wide range of species has been found unicellular as well as filamentous. Extensive areas of the McMurdo ice shelf are covered with mats of *Oscillatoria* sp., accompanied by *Nostoc* sp. (Jungblut et al. 2005). Benthic mats lining at the bottom of ice-bound pools in different areas of Antarctica are composed of *Oscillatoria*, *Lyngbya*, *Phormidium*, and *Microcoleus*. Cyanobacteria are found in all freshwater environments of Antarctica. *Phormidium* and *Synechococcus* are found in Lake Vanda. *Phormidium frigidum* develops in lakes of the Dry Valleys, sometimes together with *Lyngbya martensiana* (Vincent 2000). The nitrogen-fixing species *Nostoc commune* is abundant in Antarctic soils. Below rocks and in cracks of Antarctic rocks, *Chroococcidiopsis* can often be also found (Vincent 2000). The Antarctic cyanobacteria are not true psychrophiles as most types grow optimally at higher temperatures (15–35 °C) far above of its natural environment. Their growth rate in the cold polar regions is therefore very low. They survive to a large extent based on their tolerance to desiccation, freezing, adapt to low nutrient levels, often to highlight and UV radiation, and the lack of significant levels of predation.

1.2.3 Halophilic Cyanobacteria

Presence of high concentrations of salts does not preclude the occurrence of oxygenic photosynthesis, and some cyanobacteria thrive in concentrations up to saturation. Cyanobacteria are prominently among the phototrophic biota, found in hyper saline environments such as salt lakes, hyper saline lagoons, and solar salt pans. Many highly salt-requiring and salt-tolerant species, unicellular as well as filamentous, have been described from such environments. A general review of the occurrence and properties of halophilic cyanobacteria was reported by Oren (2000). One of the most widely occurring filamentous species is *Microcoleus chthonoplastes*, a benthic mat-building species, found worldwide up to salinities of 200 g/l and higher (Javor 1989). Another type of filamentous cyanobacterium widely encountered in high-salt environments is the coiled *Halospirulina tapeticola* (Nübel et al. 2000). The most widespread and best-known unicellular halophilic cyanobacterium is *Aphanothece halophytica*. In the Great Salt Lake (Utah, USA) cyanobacteria are a

characteristic component of the lake's biota. *A. halophytica* is found up to the highest salinities. In addition, filamentous species such as *Phormidium*, *Oscillatoria* as well as *Microcoleus*, *Spirulina*, and *Nodularia*, were found in the shallow sediments of the lake (Post 1977). A varied community of cyanobacteria, unicellular as well as filamentous, was described from the hyper saline Solar Lake (Sinai, Egypt; salinity 80–180 g/l), both in the water column and in the benthic microbial mats (Cohen et al. 1977). Solar salt pans are also a rich source of halophilic cyanobacteria (Javor 1989). At higher salinities *Phormidium*, *Spirulina*, *Aphanothece*, and *Synechococcus* become the dominant species of cyanobacteria (Javor 1989). The cyanobacterial community, within the deposits of gypsum, found in saltpan ponds of intermediate salinity has also been well studied (Sørensen et al. 2004). Halophilic and halotolerant cyanobacteria maintain their intracellular ionic concentrations at relatively low levels, although ions such as K^+ and Cl^- can transiently enter into the cells following increases in medium salinity. Many marine and moderately halophilic species, including the abundant *Microcoleus*, produce the organic solutes. Those cyanobacteria adapted to life at the highest salt concentrations (*A. halophytica*, *Halospirulina*) produce glycine betaine as their osmotic solute. Additional solutes such as L-glutamate betaine have been reported from them (Reed et al. 1986).

1.2.4 Acidophilic Cyanobacteria

Cyanobacteria generally grow in environments of neutral and alkaline pH, and are rarely found at low pH. Brock (1973) stated in his survey that benthic and planktonic cyanobacteria were never found below pH 4–5, while eukaryotic algae proliferate even at pH-levels below 3.0. However, more recently Steinberg et al. (1998) demonstrated that acid-tolerant cyanobacteria do exist. Populations of two filamentous cyanobacteria resembling *Oscillatoria/Limnethrix* and *Spirulina* sp. were found in acidic Bavarian lakes, which are having a pH of 2.9. Interestingly, eukaryotic phytoplankton was almost absent in that lake. Moreover, a survey of hundreds of lakes in Sweden and Canada showed that cyanobacteria are always present even in the most acidic lakes, down to a pH of about 3.7. Cyanobacteria such as *Aphanocapsa* sp. and several *Chroococcus* sp. have been found to dominate acidified Canadian lakes (Steinberg et al. 1998).

1.2.5 Alkaliphilic Cyanobacteria

The soda lakes of East Africa provide ample documentation for the existence of cyanobacteria adapted to life in highly alkaline environments. In these lakes, *Spirulina platensis* may reach very high community densities and high primary productivity at pH values of 11 and above (Grant and Tindall 1986). Other species, such as the heterocystous *Anabaenopsis* (*Cyanospira*) and unicellular types such as *Synechococcus* and *Gloeocapsa*, are also reported (Boussiba et al. 2000). *Gloeotheca*

linaris and *Microcystis aeruginosa* have their optimum pH near 10, and growth of *Plectonema nostocorum* was reported up to pH 13, the highest pH at which life has been recorded. *Spirulina platensis* is an obligate alkaliphile which grows best at pH 9–10 and still grows at 80% of its maximum growth rate at pH 11.5. It has been established that Na^+ is involved in pH homeostasis through the activity of Na^+/H^+ antiporters (Boussiba et al. 2000).

1.2.6 Heavy Metal Tolerant Cyanobacteria

Cyanobacterial cells can be viewed as a natural ion exchanger because they have many anionic groups on their cell surface (Kratochvil and Volesky 1998) and thus enable them to fix metal ions, mainly by means of an ion-exchange mechanism (Schiewer and Volesky 1996). The response of cyanobacteria to toxic metals have been investigated and some of these taxa have been found to display tolerance to toxic metals (Fiore and Trevors 1994). The mesophilic cyanobacteria *Anabaena flos-aquae* and *Synechococcus cedrorum* were grown in various concentrations of carpet industry effluent. The zinc tolerant strain of *Anacystis nidulans* displayed a zinc uptake comparison to a sensitive wild type. *Nostoc microscopium*, *Nostoc linckia* and *Synechocystis* sp. forms the bloom and are quite tolerant to the toxic metals, copper, cadmium, lead, and zinc.

Several cyanobacterial strains possess, outside of their outer membrane, additional surface layers, mainly of polysaccharidic in nature and referred to as a sheath, capsule, and slimes. Exopolysaccharide producing cyanobacteria could be used for metal biosorption, since most of the polysaccharide envelopes that surround cyanobacterial cells are anionic (De Philippis et al. 2001). Recent studies reported that the capsulated biomass of two filamentous cyanobacteria *Cyanospira capsulata* and *Nostoc* PCC 7936, have the good metal sorption capacity and survive in industrial effluent having multimetal system (De-Philippis et al. 2003). The cyanobacterial cells surrounded by thick polysaccharidic capsules or slime possess a large number of binding sites for metal ions compared to noncapsulated strains. Most cyanobacterial polysaccharides have abundant uronic acid subunits (De-Philippis and Vincenzini 1998) which, owing to their carboxyl groups (Urrutia 1997) efficiently binds metal ions. Thus, the use of the biomass of RPS-producing cyanobacteria for trapping metal ions seems quite promising.

1.2.7 Radiation-Resistant Cyanobacteria

Like other phototrophic organisms, light is obviously essential for cyanobacteria but at very high intensities an unbalanced absorption and utilization of the energy may occur. For instance, exposure to full sunlight at midday may cause over-excitation of the photosynthetic apparatus and cause damage to it as well as to other cellular components. Triplet chlorophyll molecules and oxygen radicals will cause photoin-

hibition and lead to oxidative damage. This is especially happening when the light includes UV wavelengths. These high-energy shorter wavelengths are deleterious and lead to oxidative stress, DNA damage, and mutations. Many species of cyanobacteria appear to be highly specialized organisms and can tolerate high solar and UV radiation. There are also few cyanobacteria belonging to this genus *Chroococcidiopsis* are extremely resistant to X-ray irradiation (Billi et al. 2000). The bases of the resistance against X-ray irradiation were the capability of *Chroococcidiopsis* to very effectively and rapidly repair DNA damage. Cyanobacteria originated early during precambrian era, i.e., before the existence of the present ozone shield, hence, it is presumed that they faced more intense solar UVR as compared to other phylogenetically much younger phototrophs. UV-B exposure had negligible short-term effects on the growth of *Nostoc. commune* (Ehling-Schulz et al. 1997). Quesada et al. (1999) found decrease in phycocyanin/chlorophyll-a and increase in carotenoid /chlorophyll -a with response to UV-A and UV-B in *Phormidium murrayi* a mat forming cyanobacterium isolated from ice self pond in Antarctica and even after 6 h of UV radiation there was almost no change in its morphological features. *Lyngbya aestuarii* from Chilika Lake, India is also quite tolerant to UV-B irradiation and have an efficient adaptation strategy to tolerate, long-term UV-B irradiation (Rath and Adhikary 2007). *Lyngbya majuscula* another mat forming cyanobacteria from saline soil also tolerant to UV-B and its metabolic activities were considerably revived after incubating the irradiated cells in mineral medium under fluorescent light and in the dark suggesting existence of photoreactivation and dark repair in this cyanobacterium (Mandal et al. 2011).

Radiation damage can be attributed by reactive oxygen species (such as singlet oxygen) formed at high light intensities. Cyanobacteria often grow on walls and pavements of building and historic monuments are exposed to full sunlight. Some of the most extreme levels of radiation that cyanobacteria encounter are found in Antarctica, where degradation of the ozone layer has brought about an increase in the amount of solar ultraviolet radiation that reaches the surface (Vincent 2000). Chlorophyll-a is the essential molecule for nearly all oxygenic photosynthetic organisms, from cyanobacteria to higher plants, excluding the Chlorophyll d-containing cyanobacterium, *Acaryochloris marina* (Chen et al. 2005). *Acaryochloris marina* is the only cyanobacterium reported that uses chlorophyll-d as its major photosynthetic photopigment. It is found in filtered light environments in various ecological niches. The advantage of using Chlorophyll-d and long wavelength absorbing chlorophylls in cyanobacteria is intriguing due to its unique absorption properties and its potential for increased photosynthetic efficiency. *Acaryochloris marina* uses Chlorophyll-d, up to 95–99% of total chlorophylls, as its major photopigment (Miyashita et al. 1996). Chlorophyll-d can replace all functions of Chlorophyll-a in *A. marina* not only in light-harvesting complexes (Chen et al. 2002; Tomo et al. 2011), but also in reaction centers (Chen et al. 2005; Tomo et al. 2007). Recently chlorophyll gets an *f* from cyanobacteria. The newly discovered cyanobacterium *Halomicronema hongdechloris* which contains Chlorophyll *f* was isolated from stromatolites found in Shark Bay, Western Australia, and cultured in the laboratory (Li et al 2014). Chlorophyll *f* from this cyanobacterium has a maximum Q_y absorp-

tion peak at about 706 nm and a maximum fluorescence emission at 722 nm at room temperature in methanol, making it the most red-shifted chlorophyll discovered to date (Chen et al. 2010). This finding suggests that cyanobacterial photosynthesis can be extended further into the infrared region.

1.3 Survival Strategy of Extremophilic Cyanobacteria

Cyanobacteria have developed an array of exceptional qualities and responses to ensure their survival in the extreme climatic conditions in which they grow. The presence of so many unique characteristics in some of these organisms creates difficulties for researchers to study only one trait without considering the effects of another. Cyanobacteria use mostly three different types of strategies to counteract extreme environmental conditions, these are: (a) stress avoidance mechanisms, (b) stress defense activities, and (c) repair mechanisms including DNA repair (Pattanaik et al. 2007).

1.3.1 Avoidance Mechanism

Under the avoidance mechanism extremophilic cyanobacteria follows four different adaptation strategies to counteract stress, i.e., migration, mat formation, change in morphology, and formation of extracellular polysaccharides. Cyanobacteria are the most successful mat forming organisms. They are closely associated with the substrate-producing mat like structure. These are of various thicknesses ranging from a few micrometers to a few millimeters. The mats are composed of a varying number of different cyanobacteria (10–40 species) (Büdel 1999). They have wide range of metabolic capabilities to adapt to extreme environmental conditions (high temperature, high light intensity, high humidity, and low water availability), prevailing in alkaline hot springs (Miller et al. 1998), Arctic fresh waters (Quesada et al. 1999), hot, arid areas (Scherer et al. 1984), rock surfaces of hot deserts (Friedmann 1967), on the bark surface (Sinha et al. 1999), rice fields (Adhikary and Sahu 2000), and on exposed rock surfaces (Pattanaik and Adhikary 2002). Generally large filamentous cyanobacteria colonize first. They possess thick sheath or slime around the filament. Composition of the microbial mat varies according to different environmental conditions and the nature of the substratum. Under extreme conditions they develop morphological and physiological adaptation that allow them to remain viable and dormant in desiccated state and under high temperature during summer months (Kovacik 2000). According to Belnap et al. (2001), the crust formation is a result of intimate association between the substrate and the microorganisms, which live within or immediately on the top of the uppermost layer. Dry cyanobacterial crusts were moistened osmotically at different water potential (Pattanaik et al. 2007).

To escape from different extreme stress condition, cyanobacteria in the mat often migrate downward and vertically depending upon the conditions of the environment. Ramsing and Prufert–Bebout (1994) reported downward movement of motile oscillatorian cyanobacteria from microbial mat surfaces into the mat matrix or into soft sediments during period of high solar irradiance. Sinking and floating behavior by gas vacuoles in the cyanobacteria act as a protective strategy against UV radiation (Reynolds 1987). In Antarctic cyanobacteria there are substantial differences between closely related species to escape damaging effects. During continuous daylight of the Antarctic summer, the motile trichomes of *Oscillatoria priestleyi* remain at the bellow of mat surface and only rise to the surface if the mat is subjected to prolonged hours of shading (Vincent and Quesada 1994). Daily vertical migration to avoid periods of incident high solar irradiance has been reported for *Oscillatoria* species and *Spirulina* ef. *subsala* (García–Pichel et al. 1994). UV irradiance is the primary cause of the vertical movement of cyanobacteria (García–Pichel and Castenholz 1994). Downward movement occurred not only in UV-B but in response to high intensities of UV-A (more than 10 W/m²) and broad visible irradiance over (400 W/m²).

Stress can also affect the motility and photo-orientation of cells and alter the morphology through breaking and changing the cyanobacterial filament to spiral or coiled structure (Rath and Adhikary 2007). However, cyanobacteria living under high levels of solar radiation, implying that they must possess efficient mechanisms to counteract the harmful effects of UVR. Though there are few studies on physiological responses of cyanobacteria to UV radiation, little has been documented on morphological modifications caused by UVR (Mandal et al. 2011). Significantly shorter trichomes were found in cultures exposed to high solar radiation. However, most of the breakage and spiral alteration occur with UV-B (Gao et al. 2007). The damage caused by UVR decreases with increase in temperature ranging from 15 to 30 °C (Gao et al. 2008). However, Zengling and Gao 2009 demonstrated that it was PAR which caused the spiraling of *A. platensis* to tighten and the presence of UVR accelerated this compressing process suggested that the self-shading provided by the compress spirals to photoprotect against harmful radiation (Wu et al. 2005).

Several cyanobacterial strains possess, outside their outer membrane, additional surface layers, mainly of polysaccharide in nature and referred to as sheath, capsule, and slimes. During cell growth in batch cultures, aliquots of the polysaccharidic material of both capsule and slimes may be released as water-soluble material into the surrounding medium, causing a progressive increase of its viscosity. These water soluble released polysaccharides (RPSs), being easily recovered from liquid culture are currently attracting much interest because of their suitability for a variety of industrial purposes. Cyanobacteria have better survival capacity in desiccated condition than the other microorganisms as they release extracellular polysaccharides (EPS) when exposed to high light and desiccation which produce a matrix that stabilizes the sediment (Helm et al. 2000). The quick absorption and slow loss of water at high and low water availability have been attributed to gel like protoplasm which consequently serve as a protective mechanism to overcome long periods of drought (Potts and Friedmann 1981). The EPS—containing sheath of cyanobacteria

forms a buffer zone between the environment and the cell. There were reports that fibrillar sheath and diffuse slime layer found in many cyanobacteria are mostly composed of carbohydrates and provide protection under stress condition (Adhikary et al. 1986; Weckesser et al. 1987).

1.3.2 Stress Defense Activities

In response to various stresses cyanobacteria change their metabolic activity and synthesize various chemicals, which often summarize as chemical defense strategies. There are various chemical defense strategies of cyanobacteria and are antioxidant defense system, synthesis of stress proteins, synthesis of photo protective compounds, and production of an array of secondary metabolites. Cyanobacteria have evolved a complex defense system against reactive oxygen species (ROS) including nonenzymatic antioxidants like carotenoids, tocopherols (vitamin E), ascorbic acid (vitamin C) and reduced glutathione. Enzymatic antioxidants are superoxide dismutase (SOD), catalase and glutathione peroxidase as well as the enzymes involved in the ascorbate glutathione cycle, such as ascorbate peroxidase (APX), mono-dehydroascorbate reductase, dehydroascorbate reductase, and glutathione reductase. Carotenoids are well known for their antioxidant activity (Tarko et al. 2012). In cyanobacteria, carotenoids occur in the outer cell membrane as well as in thylakoids. During long-term exposure to high natural or artificial radiation the carotenoids and chlorophyll-*a* ratio become very high. This high ratio is the prerequisite for a broader tolerance against excessive irradiation, particularly at suboptimal temperature (Castenholz 1972), and in response to UVR (Ehling-Schulz and Scherer 1999). To counteract UV-B induced ROS, an increase in the synthesis of carotenoids in *Microcystis aeruginosa* was observed (Jiang and Qiu 2005). Carotenoids exerted their protective function as antioxidants in *Synechococcus* PCC7942 by inactivating free radicals in the photosynthetic membrane (Goetz et al. 1999). It is also reported that outer membrane bound carotenoids provided a fast active SOS response to counteract acute cell damage (Ehling-Schulz et al. 1997). The nonenzymatic antioxidants are not considered as the efficient detoxifying agents (Wolfe-Simon et al. 2005). The most important enzymes, which detoxify superoxide radicals, are the SOD family, eliminating the noxious superoxide radical anions. Different metalloforms of SOD (Fe, Mn, Cu, Zn, and Ni) protect different cellular proteins and provide an *in vivo* tool for studying cellular responses to oxidative stress (Lesser and Stochaj 1990). Under desiccation, rehydration and during UVA and UVB irradiation, an accumulation of active Fe-SOD was detected in *Nostoc commune* (Ehling-Schulz et al. 2002). APX effectively removes low concentrations of peroxides whereas catalase eliminates H₂O₂ produced under photo-oxidative conditions. High activities of APX and catalase were reported in *Nostoc muscorum* 7119 and *Synechococcus* sp. 6311 (Miyake et al. 1991). One and two-years-old dry mats and the corresponding organism *Lyngbya arboricola* exhibited an enhancement in the

Extremophilic Cyanobacteria For Novel Drug
Development

Mandal, S.; Rath, J.

2015, VII, 92 p. 1 illus., Softcover

ISBN: 978-3-319-12008-9