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Surbhi Kharwar
Department of Botany,
University of Lucknow,
Lucknow, Uttar Pradesh,
India

Correspondence Author;
Surbhi Kharwar
Department of Botany,
University of Lucknow,
Lucknow, Uttar Pradesh,
India

Cyanobacterial photosynthetic adaptations present in Polar Regions

Surbhi Kharwar

Abstract

Cyanobacteria are the primary colonizers of every possible habitat ranging from hot to cold ecosystems. The predominant biota in the cold environment are glaciers, ice shelves, glacial melt water streams, and ice-capped lakes. To withstand such extreme environmental condition, they adapt several strategies which are known to play a crucial role in overcoming the challenges. Researchers have reported different survival strategies are adopted by these cyanobacteria such as modulations in the growth, photosynthetic processes, production of extracellular polymeric substances, carbon metabolism, produce compounds like membrane proteins, antifreeze proteins, antioxidants, secondary metabolites, and many more. However, the detailed understanding of the adaptive strategies of cyanobacteria in the photosynthetic pathway to cope with these niches has been overlooked. Therefore, the present literature review highlights the recent findings in photosynthetic adaptations in cyanobacterial species inhabiting polar regions.

Keywords: Adaptations, Cyanobacteria, polar regions, adaptive mechanisms, ecophysiology

Introduction

Cyanobacteria are photosynthetic prokaryotes are quantitatively among the most significant organisms on Earth. These organisms are Precambrian in origin, dating back approximately 3500 million years ago. In the Proterozoic, often known as the "age of cyanobacteria" which lasted between 2500 and 540 million years ago, and marked the transition from being anoxic to oxygenic photosynthesis [1-3]. They are gram-negative photoautotrophic microorganisms and are found every possible habitat [4] which can encounter several environmental conditions to abiotic or biotic stresses; consequently, have different adaptive mechanisms. They play an important role in the carbon and nitrogen economy of the ecosystem [5].

It is very interesting to know that the north and south Polar Regions of the Arctic and Antarctica together make up roughly 20% of the Earth's surface, the oceans cover about 70% of it, and the mountainous, alpine regions of Asia, Europe, North America, and South America make up the remaining 5 percent [6]. In the Polar regions, terrestrial and aquatic ecosystems have extreme environments which provide a unique chance to investigate the principles of adaptation to such extreme environments [7-11].

Cold stress is an important stress and the mechanisms by which cyanobacteria inhabiting such stressful niches respond to such condition are of great interest. Cyanobacteria living in the polar and arctic regions suffers from salinity, osmotic, freezing, low nutrients, and low-temperature stress [12, 13]. Various kinds of habitats exist in the cold environment in the different cyanobacterial species are present (Table 1). These are epilithic and hypolithic i.e., living at the rock surfaces and soil-rock interface, respectively, while endolithic are those organisms which inhabiting the interior surface of rocks [14, 15]. Persistent low temperature which characterizes polar habitats and the absorption of too much light at low temperature cause an energy imbalance resulted decreases photosynthetic performance and has negative impact on growth and affect long-term survival [24, 25]. Psychrophiles are naturally evolved to cold regions, and they normally require temperatures below 15 °C for optimal growth and temperatures between 18-20 °C for survival [26]. The term “photospychrophiles” was introduced by Morgan-Kiss and colleagues [27]. As the name suggest, psychrophiles are those organisms that are obligately adapted to low temperature i.e., 0º-15 ºC, but usually die at higher temperatures (≥ 20 ºC). They can be used to understand the physiological, biochemical, and molecular mechanisms underlying adaptation to extreme conditions. Additionally, they also provide information about exobiology i.e., possibilities for life on the other planets.

Table 1: List of reported cyanobacterial species inhabiting in the polar regions.

S. No.	Habitats	Cyanobacteria	References
1	Epilithic environment	*Calothrix* sp., *Chamaesiphon* sp., *Chroococcidiopsis* sp., *Cyanothece* sp., *Homoeothrix* sp., *Myxosarcina* sp., *Nostoc* sp., *Phormidium* sp., *Pleurocapsa* sp., *Gloeocapsa* sp., *Scytonema* sp., *Stigonema* sp., and *Synechococcus* sp.	[16]
2	Hypolithic environment	*Chroococcidiopsis* sp., *Aphanothece* sp., *Calothrix* sp., *Lyngbya* sp., *Nodularia* sp., *Nostoc* sp., *Phormidium* sp., *Plectonema* sp., *Pleurocapsa* sp., *Scytonema* sp., *Tolypothrix* sp., and *Synechococcus* sp.	[17, 18]
3	Endolithic environment	*Aphanocapsa* sp., *Aphanothece* sp., *Chroococcidiopsis* sp., *Anabaena* sp., *Calothrix* sp., *Cyanothece* sp., *Eucapsis* sp., *Hormathonema* sp., *Homoeothrix* sp., *Leptolyngbya* sp., *Lyngbya* sp., *Microchaete* sp., *Microcoleus* sp., *Nodularia* sp., *Gloeocapsa* sp., *Oscillatoria* sp., *Nostoc* sp., *Phormidium* sp., *Plectonema* sp., *Pleurocapsa* sp., *Schizothrix* sp., *Stigonema* sp., *Tolypothrix* sp., and *Synechococcus* sp.	[16]
4	Biological soil crusts	*Chroococcus* sp., *Gloeocapsa* sp., *Leptolyngbya* sp., *Microcoleus* sp., *Nostoc* sp., *Phormidium* sp., and *Scytonema* sp.	[19-22]
5	Cryoconites	*Leptolyngbya* sp., *Crinalium* sp., *Phormidium* sp., *Aphanothece* sp., *Aphanocapsa* sp., *Gloeocapsa* sp., *Synechococcus* sp., *Nostoc* sp., and *Phormidium* sp.	[23]

Contrastingly, the term “psychrotolerant” or “photo psychrotolerant” are used for those organisms that grow maximally at ≥ 20 °C but can also survive and acclimatize at 0-5 degree Celsius [26]. Photopsychrophiles are stenotherms i.e., grow and survive only over a narrow range of temperature, while photopsychrotolerant are eurytherms means growth and survival broad temperature range [28].

Depending on the particular arctic ecosystem, this might also be accompanied low-temperature conjugation with change in light intensities, annual photoperiod, and altered salt and nutrition levels [24].

Various physiological processes such as photosynthesis, respiration, nitrogen metabolism, membrane thermostability, and osmoregulation are dramatically affected by stress conditions in the cyanobacteria living in Polar Regions. The most common effects on cyanobacterial physiological responses such as growth, photosynthesis, membrane stability, and many more are shown in Figure 1.

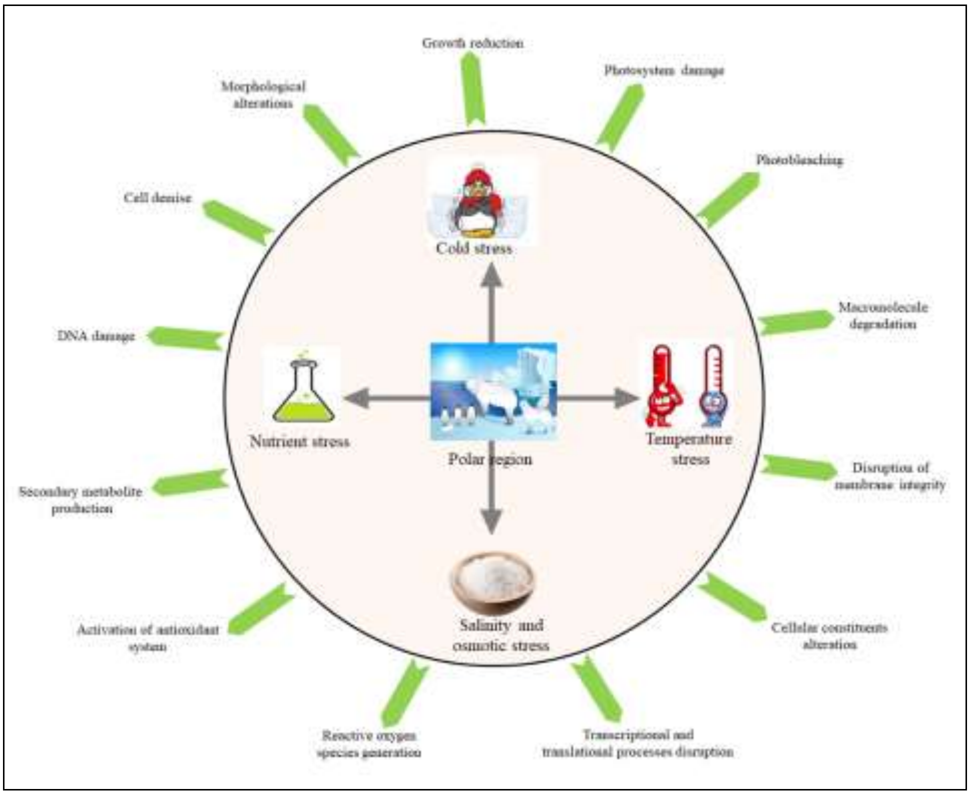

Fig 1: The common effects on cyanobacterial physiological responses inhabiting the polar regions.

To cope with such conditions, they have evolved several sophisticated mechanisms to respond to stress conditions. For example, several basic physiological processes of cyanobacteria including photosynthesis, respiration, nitrogen metabolism etc. Many of the research articles has been focused on the cyanobacterial cellular metabolisms from physiological to molecular responses. Here, we focus on the modulations in the photosynthetic process and the mechanisms underlying the polar cyanobacterial strains.

Photosynthetic Responses of Cyanobacteria Living in the Polar Regions

Photosynthesis is a process whereby light energy is gathered and stored through a sequence of chemical reactions that transform light energy into the free energy required for life. In the case of photoautotrophs, photosynthesis is the mechanism that gives access to a relatively constant external energy source in the form of sunlight. This process includes two reactions i.e., light and dark reactions [29]. Light absorption, electron transfer, and photophosphorylation are the three phases of the light reaction that occur on the thylakoid membranes. Pigments, primarily chlorophyll, in photosystem I (PSI) and photosystem II absorb light (PSII). Thereafter, light energy is transformed into nicotinamide adenine dinucleotide phosphate (NADPH) and adenosine triphosphate (ATP), which are employed in the dark reaction i.e., carbon reduction pathway, after first being converted to electron energy in PSI and PSII. Four main protein complexes namely PSI, PSII, cytochrome b6f complex (cytb6f), and ATP synthase, are responsible for catalysing this process.

Chlorophyll (Chl) is a crucial biological ingredient in the process of photosynthesis and is responsible for absorbing, transporting, and converting light energy. Only a small portion of Chl *a* is engaged in light conversion, while majority of Chl *a* and all Chl *b* participate in light absorption and transport. Numerous studies have demonstrated that as Chl *a* content rises, photosynthesis also does [30]. Light energy absorbed by Chl has three possible outcomes: it can be used to power photosynthesis (photochemistry), it can be dissipated as heat, or it can be re-emitted as light chlorophyll fluorescence [31].

The study of organisms such as cyanobacteria from extreme environment such as arctic habitats enables us to gain an understanding of resilience and phenotypic plasticity of the inhabitant cyanobacterial species which made possible by long-term evolution in harsh conditions. Research on cold-adapted polar cyanobacterial species can offer hitherto unheard-of insights into the evolution and adaptation to such severe, extreme environments over the past 100 million years.

What physiological, biochemical, and molecular adaptations in the photosynthetic process occur in the polar cyanobacteria to persist such an extreme condition?

Cyanobacteria absorb light by using photosynthetic pigments which are bonded to complexes of light-harvesting pigment and proteins. Energy is then transmitted to photosystem I (PSI) and photosystem II (PSII) reaction centres, where it is photochemically oxidised into electrons by P700 and P680, respectively, through the process of photochemical oxidation. Cyanobacteria utilizes phycobilisomes i.e., rod-like structures present on the thylakoid membranes which are responsible for the light-harvesting complexes. Phycoerythrin, phycocyanin, and allophycocyanin are proteins that are bound to form phycobilisomes.

Balancing of energy flux absorbed photon is a major challenge for all the photoautotrophs exhibiting in the thermodynamically inhospitable environment [32, 33, 25]. Changes in cyanobacterial pigmentation indicate a photoprotective mechanism to the stress environment and typically occur as a result of changes in the structure and composition of the phycobilisomes, which affects cyanobacterial light-harvesting efficiency in response to excessive excitation energy (EEE). A cyanobacterial carotenoid called myxoxanthophyll, which is found in the cell wall/cell membrane probably protects the photosynthetic system from EEE, accumulated along with the decline in the light-harvesting efficiency.

EEE results in photoinhibition of photosynthesis in extreme environments leads an imbalance in the energy of microorganisms [34]. Photoinhibition damages reaction centres of PSII and the process is reversible slowly due to the resynthesis of polypeptide of PSII reaction centre i.e., D1 protein (*psbA*). Therefore, maintaining such cellular energy flux is called photo-stasis acquired by some microorganisms [35]. Detection of such imbalance was inferred by increased excitation pressure which is assessed in terms of relative reduction state of photosynthetic electron transport chain (PETC) [36].

The preservation of photo-stasis, which involves reconstructing and reorganising photosynthetic machinery, is a major significant problem for all the microbes native to the polar areas. Similarly, cyanobacteria also remodel and restructure their photosynthetic pathway. Cyanobacterial PETC's redox status controls remodelling of photosynthetic machinery in response to variations in light, temperature, and nutritional status [37-39]. Thus, photosynthesis is an important environmental redox sensor for phototrophs. Dynamic photoinhibition is thought to be photoprotective and involves nonphotochemical quenching (NPQ) processes linked to either light-harvesting antenna complexes or PSII reaction centres [40-44].

Being the predominant phototroph in the glacial cryoconite holes, cyanobacteria also predominate in Arctic and Antarctic freshwater lakes and streams as consortia in the form of microbial mats. The presence of cyanobacteria in cold Open Ocean is comparatively less than such habitats [45, 46].

A complex and unique mechanism of adaptation to survive in cold and polar environments has been reported in cyanobacteria due to their photosynthetic nature and their requirement to maintain photo-stasis and temperature-dependent signalling pathway. A photoprotective response to EEE, phenotypic plasticity in cyanobacteria is reflected i.e., changes in the pigmentation and modulation in phycobilisome structure and composition, which lowers the capacity to gather light and maintain photo-stasis by modifying PSII [47-50].

Additionally, some of the cyanobacterial strains contain a unique protein called orange carotenoid protein (OCP). Phycobilisomes absorb excess energy, which enhances non-photochemical energy dissipation in the form of heat and photoprotection against EEE. In order to quench excess energy absorbed by phycobilisomes under EEE to increase energy dissipation in the form of heat, cyanobacteria use such OCP [51]. This safeguards the cyanobacterial photosynthetic system by reducing the efficiency of energy transfer between the phycobilisome and reaction centres.

Consortia in the form of microbial mat containing cyanobacterium i.e., *Phormidium subfuscum* are isolated from lake of Antarctic on the McMurdo ice shelf and *Phormidium tenue* isolated from Arctic river (rock surface in an Alaskan riverbed) shows plasticity in the growth and photosynthetic processes in responses to temperature. Although both of the cyanobacteria isolated from polar region, but they show differential growth response. *P. tenue* grew over a wider range of temperatures i.e., 10-40 °C, while *P. subfuscum* grew in the temperature range i.e., 5-20 °C suggested *P. tenue* has greater capacity to adjust photosynthetic performance over a wider temperature range than *P. subfuscum*. This result inference that *P. tenue* and *P. subfuscumis* exhibits eurythermic and stenothermic growth, respectively [52]. Hence, stenothermal acclimatisation strategy is significantly more advantageous in environment with relatively constant seasonal temperatures, whereas eurythermal acclimation strategy may provide advantage in environments with daily temperature fluctuations shown in permanently covered in ice i.e., Antarctica ice-covered lakes [53].

The phenotypic responses to temperature in *P. tenue* and *P. subfuscum* were also different. In order to sustain photo-stasis, *P. tenue* phenotypic and photosynthetic responses to low temperatures include changes to pigment composition as well as drops in PSII. While *P. subfuscum* showed only minor changes in pigmentation in response to low temperature, *P. tenue* lowered its Chl *a* concentration in response to decreased growth temperature, which reduced its ability for light harvesting capacity and light usage efficiency [52].

The same response (like *P. tenue*) has been documented by Miskiewicz and his colleagues in eurythermal filamentous cyanobacterium, *Plectonema organum* at low temperature [55, 45]. Several researchers have shown that Antarctic cyanobacterial strains accumulate carotenoids in conjugation with increased levels of UV-absorbing bioactive compounds such as Stoneman and mycosporine-like amino acids [52, 55, 45-47, 37]. Hence modulations in the PSII and UV-absorbing compounds (which decreases the susceptibility of cyanobacterial strains inhabiting in the Antarctic from damage due to UV radiation) are photoprotective mechanisms in cyanobacteria inhabiting in the cold aquatic ecosystems of Antarctic and Arctic [56, 57, 45]. A correlation was found between the redox-controlled accumulation of carotenoid (myxoxanthophyll) and concurrent accumulation of the UV-absorbing substances. The predominance of cyanobacteria in these harsh aquatic habitats of the Antarctic and Arctic is explained by these photoprotective mechanisms. It has been hypothesised that cyanobacteria predominate in lakes and streams of polar regions because of their sluggish but steady growth rates over several seasons and minimal biomass loss from grazing [52, 56].

Another intriguing characteristic of cyanobacterial cells is the phenomena of complementary chromatic adaptation, which is active particularly in polar locations. It has been reported that inner deeper layer has more Chl *a* than the top layer which results more pigments absorption in blue and green regions suggested the top layer communities have active protective mechanisms that facilitate photosynthesis in deeper layer [58-61]. This phenomenon of chromatic adaptation has been described in some cyanobacterial strains such as *Calothrix* sp. and *Synechococcus* sp [45, 62, 63].

Light is a limiting factor for cyanobacteria present in the polar regions. Therefore, they adapt to survive and grow in low light conditions such as high amount of Chl *a* and increased number of thylakoids indicated greater than one PS I:PS II ratio [64, 65], while opposite type of strategy has been reported in high irradiance. Recently, Dong *et al.* (2022) documented differential expression of several genes belonging to photosynthetic process such as PSI (psaA, psaB, psaC, psaD, psaE, psaF, psaJ, psaK and psaL), PSII (psbA, psbC, psbH, psbX, psbZ and psb27), cytochrome b6/f complex (*petD*), photosynthetic electron transport (petJ and petH) and light-harvesting complex (apcA, apcB, apcD, apcE, cpcA, cpcB, cpcC, cpcD, cpcE, and cpcG) in *Arthrospira* sp. TJSD091 under cold stress. The results showed that upon exposure to cold stress conditions, photosynthetic activity was decreased in the cyanobacterium, *Arthrospira* sp. TJSD091 due to the repression of differentially expressed genes [66].

Other Adaptations in Cyanobacteria Living in the Polar Regions

Myriads of complex adaptations at various levels occur in the cyanobacteria that allow their survival in an extreme polar environment such as synthesis of antifreeze proteins, exopolysaccharides, secondary metabolites, and regulation of membrane viscosity by modulation of membrane lipid and fatty acid composition by the activation of two-component histidine kinase cascade present on the cell membrane such as Hik33 kinase which regulate the expression of desaturases genes, etc. [67, 68]. Such modulation in cyanobacterial membrane at low temperatures is called as homeoviscous [69].

Conclusions

Cyanobacteria have the ability to survive different extreme conditions by adopting different strategies. Several metabolic pathways were found to be modulated under these extreme conditions. Among them, photosynthetic processes are most affected metabolism in cyanobacteria. The idea of photo-stasis in response to excessive excitation energy (EEE) is crucial to cyanobacterial acclimation as well as psychrophile adaption to cold environment. In cold environment of Polar Regions, the phenomenon of psychrophily is not necessary for survival. Different organism or different species of the same cyanobacterial genus have evolved different survival strategies. The present literature provide foundation for uncovering the survival strategies in the photosynthetic processes used by cyanobacteria during harsh conditions in the Polar Regions.

Conflict of Interest

The author declares no conflicts of interest.

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Authors Contribution statement

SK conceived and wrote the manuscript. SK reviewed, edit it and approved the manuscript.

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