Journal of Photochemistry and Photobiology B: Biology 141 (2014) 154–169

Contents lists available at ScienceDirect

Journal of Photochemistry and Photobiology B: Biology

journal homepage: www.elsevier.com/locate/jphotobiol

Short Review

Ultraviolet radiation and cyanobacteria

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ARTICLE INFO

Article history:
Received 7 October 2013
Received in revised form 22 September 2014
Accepted 25 September 2014
Available online 18 October 2014

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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http://dx.doi.org/10.1016/j.jphotobiol.2014.09.020
1011-1344/

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 ($2.8–3.5 \times 10^9$ 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].