



Review

Optimizing Light Spectrum and Intensity for Pigment Production in *Nostoc*: A Review

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Abstract

Filamentous cyanobacteria in the genus *Nostoc* show color diversity in their natural habitats, ranging from bright green to yellow–green to brown. In contrast, laboratory cultures are typically uniform in color, which is attributed to differences in light spectrum and intensity. *Nostoc* contains several bioactive pigments, including phycocyanin, phycoerythrin, allophycocyanin, carotenoids, and scytonemin, which are involved in light harvesting, photoprotection, and UV screening. Variations in light spectrum and intensity regulate the abundance and organization of these pigments, altering colony coloration and affecting photosynthetic performance, stress tolerance, and growth. These changes impact biomass and pigment productivity. In this review, we synthesize recent findings on how light regulates pigment biosynthesis in *Nostoc* and examine how wavelength, irradiance, and photoperiod influence pigment composition, biomass accumulation, and pigment productivity, considering both underlying photoregulatory mechanisms and cultivation design. This perspective connects photophysiological insights with practical strategies, including staged lighting and LED-based systems, to improve pigment yield while maintaining biomass production. These insights support the future application of *Nostoc* pigments in food, cosmetic, and pharmaceutical sectors.

Keywords: cyanobacteria; *Nostoc*; pigment biosynthesis; photoregulation; phycobiliproteins; carotenoids; scytonemin

1. Introduction

Cyanobacteria are widely known as highly adaptable, oxygenic photosynthetic prokaryotes that contribute to carbon sequestration and nutrient cycling via photosynthesis and, in many taxa, nitrogen fixation [1,2]. They thrive in diverse environments, ranging from aquatic systems to extreme habitats such as Antarctic rocks and desert crusts [3,4]. In this group, *Nostoc* species have a long history as traditional food sources and are now receiving increased attention for their biotechnological potential [5–7]. A characteristic of *Nostoc* is its ability to adjust to changing environments, which is often shown by colony color changes resulting from shifts in pigment composition [8,9]. In natural habitats, fluctuations in irradiance and spectrum, ultraviolet (UV) exposure, and desiccation drive pigment variation and color diversity, but this diversity is reduced under constant, moderate laboratory lighting conditions [3,8,10,11].

The primary pigment systems for photosynthesis and photoprotection in *Nostoc* include chlorophyll *a* (Chl *a*), carotenoids, and phycobiliproteins (PBP) [12–14]. PBPs in-



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clude phycocyanin (PC), phycoerythrin (PE), and allophycocyanin (APC). These water-soluble pigments are organized into phycobilisomes (PBSs), which function as light-harvesting antennae and enable chromatic acclimation by improving the absorption of specific wavelengths [1,12,14,15]. Carotenoids contribute to energy dissipation and antioxidant defense and are widely considered industrially relevant pigments, including for use in cosmetic applications [13,15,16]. In addition to these pigment systems, cyanobacteria produce UV- and stress-protective compounds, such as scytonemin (a sheath-associated UV-screening pigment) and mycosporine-like amino acids (MAAs), which mitigate UV-driven oxidative stress and cellular damage [9,11,17,18]. They also use carotenoid-associated proteins that protect cells under strong light, connecting pigment systems with photoprotection [19].

As these pigments and protective systems support light capture and stress protection, their production changes in response to environmental conditions. Light spectrum and intensity control chromatic acclimation, which regulates physiology and metabolism, impacting (i) pigment composition per biomass, (ii) photosynthetic performance and growth, and (iii) volumetric pigment productivity [1,14,20–23]. This is relevant for practical applications because light spectrum and intensity are controllable, and light-emitting diode (LED) systems enable reproducible, wavelength-specific cultivation strategies [1]. For example, studies on *Nostoc* cultivation have demonstrated that light quality and intensity shift pigment profiles and affect biomass formation and extracellular product production [5,24]. Stress studies highlight that UV exposure should be applied carefully because it can increase reactive oxygen species (ROS) accumulation and damage cellular machinery, reducing growth and altering pigmentation, photosynthesis, and nitrogen-related processes [9,25].

Knowledge of light-driven pigment regulation in *Nostoc* is necessary to understand the ecology and color changes in these species and to ensure the sustainable production of valuable natural compounds. *Nostoc* pigments and extracts have high value in food, cosmetic, pharmaceutical, and related industries, as they function as natural colorants and bioactive compounds with antioxidant, anti-inflammatory, antimicrobial, and anticancer potential [13,16,17,26–32]. In the food sector, cyanobacteria-derived pigments, such as chlorophylls, carotenoids, and PBPs, are used as natural colorants, and their health-related attributes further increase their value [13,27]. PBPs are even more attractive because they are water-soluble and commonly extracted using aqueous methods [14,17]. In cosmetics and skincare, cyanobacterial pigments, such as carotenoids and PBPs, are used as antioxidant and antiaging-oriented ingredients [16,33]. Moreover, photoprotective compounds, such as scytonemin and MAAs, are being explored for topical applications, including photoprotection and antiaging-oriented skincare concepts; this is consistent with the fact that UV-B is a strong oxidative stressor in aquatic photosynthetic microorganisms [9,11,18,33]. Genus-focused reviews remain necessary, as cyanobacterial genera differ in their chemical composition and applications [34].

To the best of our knowledge, few reviews have summarized how light spectrum and intensity regulate pigment biosynthesis in *Nostoc* and how these organisms acclimate to changing light environments by adjusting their pigment composition. This is important for ecology and bioprocess design [1,6,21,22]. *Nostoc* provides a valuable genus-level model, as many species are widely distributed across aquatic, terrestrial, and extreme habitats, where tolerance to desiccation, high irradiance, and UV exposure is essential [3,8,24]. Their colonies, mats, and sheathed aggregates generate internal light gradients and UV-screening microenvironments that influence color plasticity, photoprotection, and cultivation scale-up. Together, these ecological and structural characteristics are associated with specialized photoprotective systems, including carotenoid-related protection and extracellular scytonemin-containing sheaths. As pigment composition, metabolite profiles, and stress

responses vary among cyanobacterial genera, broad cyanobacterial models may not fully capture light-regulated pigment dynamics in *Nostoc*. Therefore, this review summarizes the available literature on light-regulated pigment biosynthesis in *Nostoc*, emphasizing Chl *a*, carotenoids, PBP (PC, PE, and APC), and UV-associated protective systems, and presents some light-related cultivation strategies that support the sustainable production of high-value natural pigments.

2. Pigments Present in *Nostoc*

Nostoc contains several pigments that support photosynthesis and protect cells from fluctuating light, UV exposure, and desiccation stress, including Chl *a*, PBP, carotenoids, and scytonemin. Table 1 provides a functional overview of these pigment systems, showing their location, main roles, and major light-related drivers. Thylakoid-associated pigments, including Chl *a*, PBP, and carotenoids, are mainly involved in photosynthetic light capture, energy transfer, and protection against excess excitation energy. Sheath-associated scytonemin provides an external UV-screening layer. Together, these pigments determine colony color and reflect shifts between light harvesting and photoprotection under changing environmental conditions [3,8,35].

Chl *a* is the primary photosynthetic pigment present in oxygenic cyanobacteria, including *Nostoc*. It is embedded in the thylakoid membranes and acts as the central component of the reaction centers in Photosystems I (PSI) and II (PSII), driving photochemical reactions and photosynthetic electron transport [5,36,37]. Chl *a* primarily absorbs light in the blue (approximately 430–440 nm) and red (approximately 660–680 nm) regions of the spectrum [37]. In *Nostoc*, Chl *a* levels are generally stable but can decline significantly under stress, such as high UV radiation or extreme light intensity, a process known as photobleaching [22,38,39].

PBP are water-soluble, brightly colored proteins assembled into PBS that attach to the surface of thylakoid membranes and serve as the main light-harvesting antennae, transferring excitation energy to Chl *a* [12]. Their relative composition—especially the PE:PC:APC ratio—explains many visible “color shifts” in colonies and mats and alters the excitation balance between PSI and PSII [12,40]. In PBS, PC (~620 nm) and APC (~650 nm) are core PBP that capture orange/red light and transfer energy to Chl *a* [29,41]. In contrast, PE (~560 nm) extends absorption into the green/yellow region and is often inducible, increasing under green-enriched light via chromatic acclimation, which maximizes photon capture [12,40,42,43].

Carotenoids are hydrophobic pigments embedded in thylakoid membranes and outer cellular layers. They have two main roles: light harvesting in the blue-green region (400–550 nm) and, more importantly, photoprotection through the quenching of singlet oxygen and other ROS generated under high-light stress [15,28,35,44]. Major carotenoids in *Nostoc* include beta-carotene, echinenone, and myxoxanthophyll [45]. In addition to their direct antioxidant function, carotenoids contribute to specialized protein-based photoprotective systems that regulate excess excitation energy before it cause photodamage. Specifically, carotenoid-binding proteins, including orange carotenoid protein (OCP)-related systems and their homologs, provide a regulated route for non-photochemical quenching by converting excess excitation energy into heat [15,19]. Recent studies on *N. flagelliforme* have identified “red proteins” or helical carotenoid proteins (HCPs) that bind the ketocarotenoid canthaxanthin. These proteins are structurally related to OCP and represent a distinct carotenoid–protein adaptation in this terrestrial species [19,46]. These proteins indicate that carotenoids in *Nostoc* function not only in membrane-associated antioxidant protection but also in specialized energy-dissipation systems associated with stress tolerance [19,46].

Table 1. Overview of the major pigment groups in *Nostoc*, including their cellular localization, light-absorption characteristics, and functions related to photosynthesis and photoprotection. APC = allophycocyanin; Chl *a* = chlorophyll *a*; PBS = phycobilisomes; PC = phycocyanin; PE = phycoerythrin; PSI = Photosystem I; PSII = Photosystem II.

Pigment System	Typical Location	Characteristic Absorption	Main Functional Role	References
Chlorophyll <i>a</i> (Chl <i>a</i>)	Thylakoid membranes (photosystems)	Blue (~430–440 nm) and red (~660–680 nm)	Core photosynthetic photochemistry in PSI/PSII and electron transport	[2,22,25]
Phycobiliproteins (PBPs: PE, PC, APC)	Attached to the thylakoid surface as PBS	PE (~560 nm), PC (~620 nm), and APC (~650 nm)	Light-harvesting antenna; transfers excitation energy to Chl <i>a</i> ; central to chromatic acclimation and colony color shifts	[12,14,40,42]
Carotenoids	Thylakoid membranes and, in some cases, outer cell layers	Broad visible absorption (400–550 nm)	Photoprotection (ROS quenching, energy dissipation); supports stress tolerance under high light	[4,15,19,35]
Scytonemin	Extracellular polysaccharide sheath (outside cells)	Broad UV absorption; maximum ~384–390 nm	Extracellular UV screening; long-lasting protection under UV/desiccation; reduces UV-driven damage to internal machinery	[11,18,25,47]

Scytonemin is a yellow-brown, lipid-soluble, extracellular “sunscreen” pigment located in the extracellular polysaccharide sheath of *Nostoc* and other cyanobacteria [11]. In addition to UV screening, scytonemin is also discussed in biomedical-oriented reviews as a cyanobacterial pigment with therapeutic relevance [17]. It is capable of broad UV absorption, with a maximum at approximately 384–390 nm [44], and its synthesis is often triggered by UV-A exposure and high-light/desiccation stress [46,47]. Scytonemin is chemically stable and persists in the sheath for long periods, even when cells are dormant [37]. This is particularly relevant for terrestrial and mat-forming *Nostoc*, in which desiccation cycles and intermittent irradiation repeatedly expose colonies to UV stress [3,8]. By intercepting UV-A radiation before it reaches the cell, it prevents DNA damage and photo-oxidation of the photosynthetic apparatus [47,48]. As scytonemin production can occur at the cost of growth, its induction reflects the trade-off between photoprotection and biomass accumulation.

3. Effects of Light Spectrum

Many *Nostoc* species alter their pigment composition in response to ambient light, a phenomenon known as complementary chromatic adaptation (CCA), which enables cyanobacteria to maximize light harvesting. For example, cells accumulate red-pigmented PE under green light, while they synthesize blue-pigmented PC under red light [40]. These green- and red-light responses are supported by molecular mechanisms, including sensor kinases such as CcaS, which regulate the expression of PBP genes [41,42]. In cyanobacteria, light-regulated pigment changes are mediated by photoreceptors and signaling cascades that control PBS composition and broader physiology, and chromatic acclimation is a well-studied example showing that cells adjust PBS components in response to wavelength

and irradiance [1]. Cyanobacteriochromes (CBCRs) are bilin-based photoreceptors that cover UV-visible wavelengths and distinguish closely related wavelengths, activating wavelength-specific regulatory pathways, including PBS reorganization [1]. CBCRs confer broad UV-visible sensing, and green/red sensing systems such as CcaS, link spectral signals to PBS regulation [1,41]. In *N. punctiforme*, CBCR CcaS detects green light and regulates genes involved in PE synthesis, illustrating a direct pathway from light perception to pigment output [41,42]. Mechanistically, CcaS undergoes reversible green/red photoconversion, which modulates its signaling activity, switching its regulatory output so that PE-related genes are promoted under green light and reduced under red light [1,41]. CCA also involves complex regulatory networks, such as regulator of chromatic adaptation (Rca) pathways, indicating that these pigmentation shifts experience tight genetic regulation rather than passive pigment turnover [1]. CCA is mechanistically diverse across cyanobacteria, and multiple regulatory systems, including Rca-type pathways, link light sensing to PBS remodeling, contributing to strain-dependent responses in *Nostoc* [1,40]. These pathways act as an integrated regulatory network, with CBCR/CcaS and Rca-type regulation converging on PBS gene expression and the cellular redox/ROS state (shaped by irradiance and stress) modulating the strength and stability of pigment outcomes, which explains the strain-dependent PE/PC responses under similar spectra [1,12,37,40–42]. Figure 1 summarizes how spectrum, irradiance, photoperiod, and stress signals integrate to shape pigment composition in *Nostoc*. In contrast, the effects of blue and purple light are mainly based on empirical observations and reflect condition-dependent, stress-driven photoprotection rather than a specific adaptation program [41,49]. Figure 2 and Table 2 show the impact of light on pigment composition in *Nostoc*.

Red light generally promotes Chl *a* and PC production in *Nostoc*. For example, *N. sphaeroides* grown under red light shows higher dry biomass and PC content than under other wavelengths [29], and *N. flagelliforme* exhibits increased PC content relative to APC under red light, likely to improve light absorption [24]. Because of this, red LEDs are commonly used to enhance PC accumulation and maintain productive growth; for example, red-light intensity modulation increases PC in *N. commune* [21]. Red light may also reduce the need for PE-rich antennal components compared to green light and can support efficient photosynthesis at moderate irradiance [20,22]. These observations are consistent with PBS remodeling under chromatic acclimation, in which regulatory responses shift antenna composition to favor absorption in the dominant wavelength environment [1]. This response is mediated by phosphorelay regulatory systems such as the Rca pathway, in which cyanobacteriochrome sensor kinases detect changes in red and green light and regulate the expression of PBP-related genes [40]. This suggests that red-biased spectra paired with a moderate intensity and a controlled photoperiod are often favorable for PC productivity.

Green light tends to increase PE and shift the color of *Nostoc* toward yellow–green or brown by changing the PBS. For example, in *Nostoc* sp. strain MAC, exposure to green light altered the PE:PC ratio to >2:1, and the cells became brown. In contrast, white light kept the ratio near 1:1, and the cells stayed green [12]. Green-enriched conditions generally promote PE accumulation and pigment rebalancing in cyanobacteria capable of PBS adjustment [40,42,50]. This is supported by green-light sensing pathways (e.g., CCAs/CBCR-based regulation) that upregulate PE-related gene expression in responsive strains [41,42]. Under green light, regulators, such as RcaC, promote PE gene expression and repress specific PC-related genes; under red light, this regulatory pattern is reversed, enabling dynamic PBS reorganization in response to spectral conditions [42]. In practice, green light can be used in a short “induction phase” before harvesting to obtain PE-rich biomass or extracts.

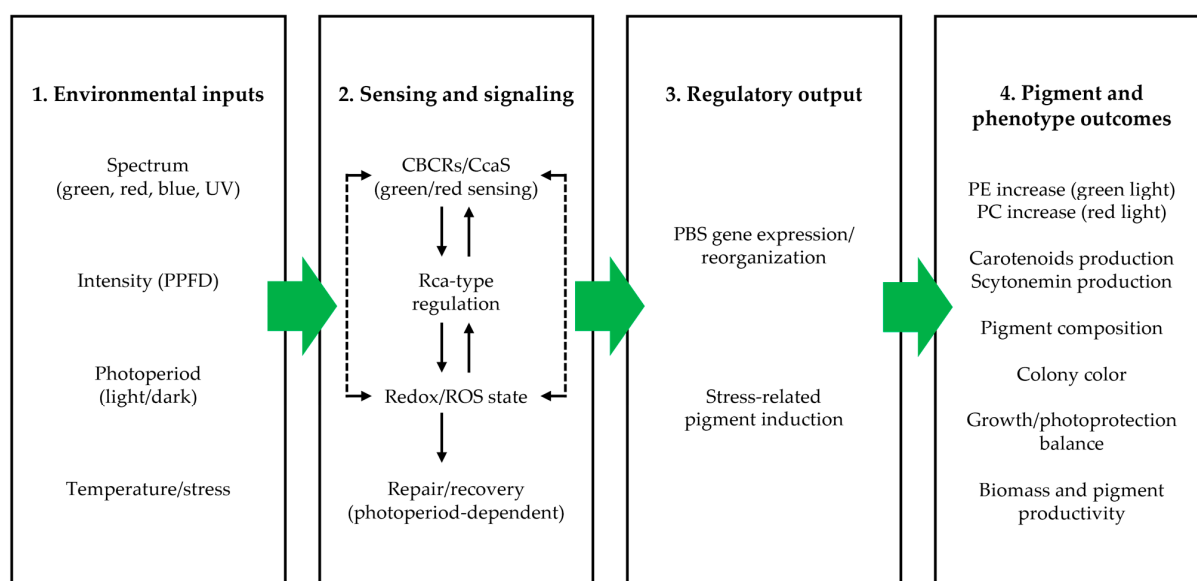


Figure 1. Integrated model showing how light spectrum (CBCR/CcaS; Rca-type pathways), irradiance-driven excitation pressure, and redox/ROS signaling jointly regulate PBS composition and pigment outcomes in *Nostoc*. CBCRs = cyanobacteriochromes; PBS = phycobilisomes; PC = phycocyanin; PE = phycoerythrin; PPFD = photosynthetic photon flux density; Rca = regulator of chromatic adaptation; ROS = reactive oxygen species.

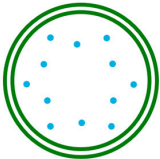
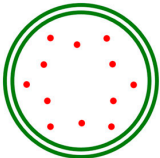
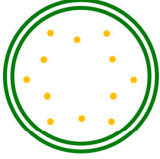
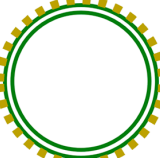
	Red light Use red-enriched light as the primary light source to increase blue phycobiliprotein production	Moderate light Keep PPFD at a moderate level to avoid pigment bleaching while still supporting pigment synthesis	Photoperiod optimization Adjust light–dark cycles to maximize pigment yield	 PC and APC
	Green light Shift to green-enriched light to induce PE synthesis	Monitor PE:PC ratio Track the PE:PC ratio as an indicator of PBS remodeling	Phycobiliprotein remodeling Green light remodels light harvesting for better green-light capture	 PE
	Blue/high-light Apply blue or high-light pulses late in cultivation to promote protective carotenoid accumulation	Control stress and nutrients Combine high light with targeted nutrient limitation to enhance carotenoid synthesis	Antioxidant response Carotenoids protect against high-light oxidative damage	 Carotenoids
	UV-A/UV-B Apply UV-A/UV-B to induce scytonemin biosynthesis, a UV-screening pigment	Scheduled recovery cycles Alternate UV exposure with recovery periods to support DNA repair and culture health	Sheath-forming conditions Favor sheath formation for scytonemin deposition	 Scytonemin

Figure 2. Light-based strategies for regulating pigment composition and improving cultivation performance in *Nostoc*. The colored dots indicate the main target pigments promoted under each light condition. APC = allophycocyanin; PBS = phycobilisomes; PC = phycocyanin; PE = phycoerythrin; PPFD = photosynthetic photon flux density.

Blue light can increase some compounds in *Nostoc*, such as total protein and PBPs, as reported for *N. sphaeroides* [29]. This increase in total protein may reflect greater PBP accumulation, as PBS/PBPs constitute a large fraction of cellular soluble proteins [14,29]. Blue light can enhance specific PBPs, such as PE, and as these light-harvesting structures may constitute up to 50% of the total soluble protein in cyanobacterial cells, their accumulation directly contributes to a higher biomass protein content [29]. However, blue light does not always favor growth. In *N. flagelliforme*, blue light (and other single-color treatments) reduced biomass compared to white light, suggesting that it may stimulate specific pigments while limiting the overall productivity when used alone [5,49]. This is often because blue light triggers stress/photoprotection responses, especially at higher intensities, increasing the excitation pressure, ROS formation, and carotenoid accumulation, depending on the species and conditions [15,35]. The effects of blue light are dependent on the conditions; at a higher intensity, it can act as a stressor, but under a moderate photosynthetic photon flux density (PPFD) and appropriate nutrient conditions, some *Nostoc* strains show increased PBPs [9,24]. In *N. sphaeroides*, increased PBPs have been reported under blue light and moderate irradiance ($\sim 30 \mu\text{mol photons m}^{-2} \text{s}^{-1}$), consistent with stimulation without bleaching-level stress [29]. Therefore, it is crucial to distinguish productive pigment accumulation from stress-induced accumulation. Optimized spectra (e.g., mixed or white light) increase pigment content and biomass, whereas monochromatic blue light increases specific PBPs but reduces the biomass and polysaccharide yield [5,49]. This distinction should be assessed considering the growth rate, Chl *a* stability (including bleaching), and ROS-related indicators [9]. Blue-light responses are often mediated by redox/ROS-driven photoprotection pathways rather than CCA-specific PBS switching, explaining condition-dependent outcomes [1,9,24,37].

In addition to light color, UV exposure is a major factor in scytonemin induction and broader stress acclimation. Enhanced UV-B can alter growth and pigment content in *N. muscorum* [25] and *N. commune* [51]. Scytonemin provides extracellular screening, and its production is associated with UV-A exposure and sheath development [47]. As scytonemin is localized in the sheath, it indirectly protects the internal photosynthetic apparatus by screening incident UV before it reaches sensitive cellular targets, reducing UV-driven photooxidation and stress on photosystems and pigments [11,47]. This mechanism is consistent with observations that UV-B reduces Chl *a* and PBPs and suppresses *Nostoc* growth, supporting the advantage of sheath-level UV screening [25,52]. In cultivation, this suggests using controlled, time-limited UV conditions rather than continuous exposure when targeting scytonemin.

Overall, these light-driven responses are often strain- and context-dependent, and differences among studies reflect the natural habitats of the *Nostoc* strains. The habitat likely contributes to variation across *Nostoc* studies because the natural environment influences a strain's pigment response. Aquatic strains often prioritize the adjustment of PBPs to capture changing underwater light spectra [12]. In contrast, terrestrial and subaerial mat-formers experience stronger UV and desiccation cycles and rely more on sheath-associated protection, including extracellular sheaths enriched in scytonemin and carotenoids, rather than primarily adjusting antenna pigments [10,44]. These ecological differences likely contribute to the strain-dependent pigment responses reported in the literature. As the habitat alters UV exposure, desiccation frequency, and optical environment, it can shift pigment strategies between PBS-based light harvesting and sheath-associated photoprotection [10–12,44]. Table 3 summarizes this habitat framework to interpret cross-study variability.

Table 2. Effects of light on pigment production in various *Nostoc* species and strains. Chl *a* = chlorophyll *a*; EPS = extracellular polymeric substances; MAAs = mycosporine-like amino acids; PAR = photosynthetically active radiation (broad-spectrum visible light, 400–700 nm) without spectral tuning; PBPs = phycobiliproteins; PC = phycocyanin; PE = phycoerythrin. Increased/decreased indicates a change relative to the control/reference condition reported in the cited study (often a white-light control under otherwise identical conditions). Biomass refers to biomass yield (typically dry weight) unless the cited study reports a different growth metric.

<i>Nostoc</i> Strain	Light Condition	Observed Effect on Pigments	Comparison (Reference Condition)	References
<i>N. sphaeroides</i>	Red light	Increased PC and dry matter	White-light control/other wavelengths in study	[29]
<i>N. sphaeroides</i>	Blue light (under moderate irradiance)	Increased PE and protein	White-light control/other wavelengths in study	[29]
<i>Nostoc</i> sp. MAC	Green light	Increased PE:PC ratio (>2:1); cells turned brown	White-light control	[12]
<i>Nostoc</i> sp. MAC	Darkness	Decreased PE and Chl <i>a</i> ; PC remained stable	Light-grown/white-light condition in study	[51]
<i>N. flagelliforme</i>	Mixed (red/green/blue)	Enhanced EPS and biomass compared to white light	White-light condition in study	[6]
<i>N. calicicola</i>	High intensity	Decreased Chl <i>a</i> , PC, PE; increased carotenoids	Lower/standard intensity	[22]
<i>N. commune</i>	UV-A/UV-B	Induction of scytonemin predominantly by UV-A and of MAAs by UV-B	No-UV control/PAR-only	[45]
<i>Nostoc</i> sp. HKAR-2	UV-B + PAR	Diurnal destruction/resynthesis of photosynthetic pigments and PBPs; carotenoid induction	PAR-only/no-UV	[52]
<i>Nostoc</i> sp.	Red LED	Intensity of 30 $\mu\text{mol}/\text{m}^2/\text{s}$ optimal for biomass	Other PPFD levels tested	[21]

Table 3. Habitat context for pigment responses in *Nostoc*. This table summarizes how habitat-driven stressors (e.g., spectral filtering, UV exposure, desiccation, and internal gradients) shift pigment strategies toward PBS-based regulation (PBPs) or sheath-associated photoprotection (scytonemin/carotenoids), explaining cross-study variability. Chl *a* = chlorophyll *a*; EPS = extracellular polymeric substances; MAAs = mycosporine-like amino acids; PAR = photosynthetically active radiation (broad-spectrum visible light, 400–700 nm) without spectral tuning; PBPs = phycobiliproteins; PC = phycocyanin; PE = phycoerythrin; PPFD = photosynthetic photon flux density.

Habitat Context (Typical Growth Form)	Dominant Light/Stress Conditions	Expected Pigment Strategy (Interpretation Lens)	Practical Measurable Indicators to Report	References
Aquatic/submerged (suspensions, thin biofilms)	Spectral filtering by water; variable light quality	PBS-based regulation dominates: pigment responses often expressed as PE $\leftrightarrow$ PC $\leftrightarrow$ APC shifts to match available wavelengths	PE:PC:APC ratio; PBP content per biomass; color shifts under wavelength changes	[8,12]
Terrestrial and subaerial mats/crusts (soil crusts, bark/rock biofilms; thick sheaths)	High UV + frequent desiccation; intermittent wetting; high irradiance episodes	Sheath-level protection dominates: stronger investment in scytonemin/MAAs and carotenoid-based protection relative to antenna expansion	Scytonemin (presence/content); MAAs; carotenoids; sheath thickness/EPS; pigment persistence during dormancy	[10,11,44,45]

Table 3. Cont.

Habitat Context (Typical Growth Form)	Dominant Light/Stress Conditions	Expected Pigment Strategy (Interpretation Lens)	Practical Measurable Indicators to Report	References
Hot-spring/high-irradiance diurnal systems	Strong daily PAR + UV cycling; temperature extremes	Dynamic damage–recovery regime: pigments may decline in light and recover in dark; photoperiod becomes a key driver	Diurnal pigment loss/recovery (PC/PE/Chl <i>a</i>); carotenoid induction; photoperiod details (light/dark)	[52–54]
Dense colonies/aggregates (any habitat; mats and clumps)	Strong internal gradients; self-shading; surface vs. interior microenvironments	Internal “effective light field” dominates: incident PPFD may not reflect cellular exposure; heterogeneity expected	Culture depth/optical path; mixing; spatial pigment heterogeneity (surface vs. interior); “effective irradiance” considerations	[3,55]

4. Effects of Light Intensity

Light intensity is another critical factor, as too little light limits photosynthesis, whereas too much light causes photoinhibition and oxidative stress [38,54]. In many cyanobacteria, moderate light often increases the pigment content per biomass, but very high light can reduce PBPs (photobleaching/downregulation) and increase carotenoids and other protective compounds [35,44,48]. For example, in *N. calcicola*, the light intensity and photoperiod affect growth and biochemical composition, highlighting the balance between productivity and stress responses [22]. Pigment synthesis depends on light–dark cycles (photoperiod) and environmental conditions [37,43]. For example, the same daily light dose leads to different pigment outcomes depending on how it is delivered—continuous light, longer days at a lower PPFD, or shorter periods at a higher PPFD [22,23]. Across studies on *Nostoc*, low-to-moderate PPFD generally ranges from approximately 20 to 100 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. In contrast, higher light intensities, particularly in combination with UV and photosynthetically active radiation (PAR), increase stress responses and protective pigment production and reduce PBPs and Chl *a* [6,9,22]. In dense cultures, self-shading reduces photodamage in inner cells but also limits light penetration, lowering overall photosynthetic efficiency and making mixing and reactor design important for high-density cultivation and scale-up [3,6,55]. Photoperiod is also crucial, as continuous light and light–dark cycles produce different effects at the same daily light dose. This is especially relevant for LED-based cultivation, as photoperiod can be adjusted to balance productivity, stress, and pigment accumulation [1,23].

4.1. Low-to-Moderate Intensity: Pigment Accumulation

Cyanobacteria generally exhibit a negative correlation between light intensity and the light-harvesting pigment content, optimizing their antennal systems to maximize photon capture under low-light conditions. This strategy of pigment accumulation ensures photosynthetic efficiency when energy is scarce. For example, *N. calcicola* prefers low light (21–63 $\mu\text{mol/m}^2/\text{s}$), under which PBPs and Chl *a* accumulate maximally; intensities surpassing this range significantly decrease the pigment content, as the cells adjust to avoid excess energy absorption [22]. Similarly, *N. sphaeroides* requires a specific moderate intensity of roughly 90 $\mu\text{mol/m}^2/\text{s}$ to optimize PBP yield, which has been reported as the pigment content per biomass (mg gDW^{-1}) and/or pigment productivity ($\text{mg pigment per g dry biomass}$), depending on the study, with production dropping at higher or lower intensities, indicating the precise window for optimal biosynthesis [29]. This behavior is consistent with findings in other *Nostoc* species, in which low light acts as a stimulant for PC and PE synthesis to broaden light harvesting and high light triggers their degradation [56]. Overall,

previous studies have suggested an effective irradiance range for PBP accumulation and biomass production, typically within 30–90 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. This includes for *N. calicicola* (~21–63), *N. commune* (~30), and *N. sphaeroides* (~90), for which high PBP yields can be achieved without photoinhibition [21,22,29].

4.2. High Intensity: Photoinhibition and Photoprotection

Exposure to high light intensity (99–250 $\mu\text{mol/m}^2/\text{s}$, depending on the specific cyanobacterial species) acts as a stressor that induces photoinhibition and activates photoprotective mechanisms to prevent oxidative damage [11]. Under these conditions, *Nostoc* species often undergo “bleaching”, a regulated reduction in light-harvesting pigments, such as PE and PC, to limit excess photon absorption [38]. Photoinhibition is closely linked to PSII damage and repair. Under continuous high light exposure, ROS can damage the D1 protein of PSII, increasing the need for efficient repair cycles [38,48]. When damage exceeds repair capacity, photosynthetic efficiency is reduced, and bleaching may occur [48]. Carotenoids and extracellular scytonemin can reduce ROS formation and protect the photosynthetic apparatus under excess light [38]. Simultaneously, cells regulate the synthesis of carotenoids, which serve as non-enzymatic antioxidants that quench ROS generated by over-excited photosystems. For example, in *Nostoc* sp. strain HKAR-2, exposure to high PAR combined with UV-B radiation reduces Chl *a* but increases carotenoids [52]. At irradiances above ~100 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, cells often shift from light harvesting to photoprotection. In some cases, high irradiance may promote extracellular UV-screening mechanisms, such as scytonemin accumulation [11]. Under extreme light exposure of up to ~500 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, PBP photobleaching has been observed, whereas antioxidant carotenoids may contribute to oxidative stress mitigation [38]. When high irradiance is accompanied by desiccation, the photoprotective response is associated with survival under dormancy-like conditions. In terrestrial *N. flagelliforme*, HCP accumulation has been reported under combined stress conditions, suggesting that these OCP-related proteins complement pigment reduction and carotenoid accumulation by providing an additional route for dissipating excess energy [19,46]. Thus, in the context of light intensity, HCPs are not simply carotenoid-binding proteins but part of a high light and desiccation-response strategy that protects photosynthetic structures during severe environmental stress [19,46]. From a cultivation perspective, these patterns suggest that PPFD should be maintained below ~90 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ when PBPs are the target products and that applying higher irradiance, often as a secondary stress phase, will enrich protective compounds, such as scytonemin [11,21,22]. Dark recovery may also mitigate high light-induced pigment loss; in *Nostoc* sp. strain VKB02, PC and PE decreased under high intensity PAR/UV exposure but recovered during the subsequent dark phase [54].

5. Two-Step Culture to Promote Pigment Biosynthesis

Two-step culture (a growth phase followed by a targeted induction phase) is a practical method for improving the commercial pigment yield of *Nostoc* because it separates two competing objectives; efficient biomass accumulation and pigment biosynthesis, which often requires stress (Figure 3). In a single-stage method, continuous exposure to induction conditions (e.g., UV, high light, or certain monochromatic spectra) stimulates specific pigments but frequently reduces overall energy capture, damages light-harvesting complexes, and reduces biomass productivity. A two-step method reduces this risk by enabling cultures to accumulate biomass before applying controlled induction (light spectrum shifts, intensity increases, and/or UV exposure) to increase pigment biosynthesis [21,22,25,36,46,47]. This trade-off may be relevant in *Nostoc*, as colony and mat structures generate internal light gradients, which restrict induction light from reaching deeper biomass layers [3,6]. At scale,

this becomes a bottleneck because dense aggregates, biofilms, and extracellular sheaths cause strong light attenuation, and single-cell light-distribution assumptions underestimate internal shading in *Nostoc* [55].

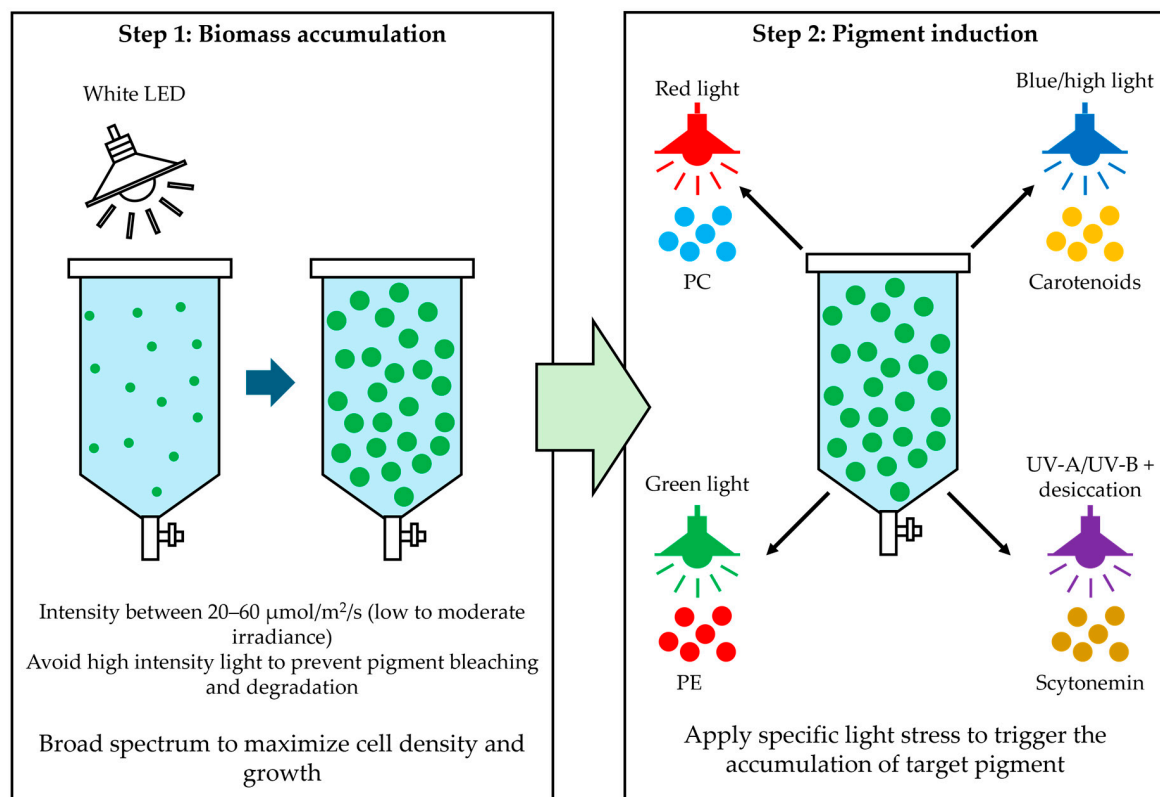


Figure 3. Schematic representation of a two-step cultivation strategy. Step 1 involves biomass accumulation and Step 2 promotes pigment induction under controlled light conditions. The different light colors indicate specific light conditions, while the colored circles represent the main pigments promoted under each condition.

In Step 1, the biomass production phase, cultures are maintained under conditions that favor photosynthesis and rapid growth—commonly broad-spectrum or red-enriched light at low-to-moderate PPFD—increasing biomass and cell density. Moderate irradiance (e.g., $\sim 21\text{--}63 \mu\text{mol}/\text{m}^2/\text{s}$) supports growth and maintains Chl *a* and PBP levels [22], and moderate-intensity red light promotes PC accumulation without driving chronic oxidative stress [21]. As PBPs are sensitive to long-term high light exposure, Stage 1 should minimize continuous photoexcitation stress, which causes pigment bleaching or degradation, to produce sufficient biomass for the subsequent induction step [35,44,48]. As the culture density increases, self-shading can intensify these gradients, making reactor design and mixing critical for maintaining uniform light exposure [3,23,30]. For industrial scale-up, quantitative modeling of the internal photon field can estimate how PPFD decays in dense cultures and identify an effective culture depth; wavelength-specific attenuation models have been applied to *Nostoc* to improve biomass prediction under self-shading [50].

In Step 2, pigment induction occurs during a controlled light stress phase, following biomass accumulation, and the light is intentionally changed to enrich the target pigments using the wavelength and/or irradiance as specific induction signals. For PC production, maintaining a red-biased spectrum and adjusting irradiance can be effective, as shown for *N. commune* under red LEDs [21]. For PE, a green-enriched induction step is supported because chromatic acclimation remodels PBPs to improve green light harvesting and increase PE compared to other PBPs [40,42]. For carotenoids, induction is associated with increased

excitation pressure (e.g., short high light and/or blue-enriched phases), consistent with the functions of carotenoids in energy dissipation and ROS quenching under photooxidative conditions [4,15,35]. Scytonemin is induced by UV-A/UV-B exposure, especially when combined with high light and desiccation [11,45,53,57]. However, extended UV exposure can degrade PBPs, damage DNA, and suppress growth [25,52]; thus, prolonged UV treatment may result in low biomass or culture failure. In contrast, in a two-step method, biomass is first accumulated under adequate nutrients, and then, a short UV/high-light induction phase is applied to promote scytonemin production (often alongside carotenoids) without compromising productivity. Thus, the effectiveness of the induction step depends on whether light reaches the whole culture or remains limited to the surface layers, which is an important consideration for scale up [3,6]. To scale-up *Nostoc* cultivation, reactor design should reduce self-shading using shallow culture layers and sufficient mixing so that cells move between bright and shaded zones [6,55]. In addition, lighting settings (spectrum, PPFD, and photoperiod) and basic culture configuration (e.g., depth/optical path) should be reported to support comparisons and reproducibility [1,23]. In *Nostoc*, scale-up is constrained by colony/mat morphology, which creates internal light gradients [3,55]. As biomass accumulates, the surface layers can receive induction light (red/UV), and deeper layers may remain under low-light conditions. Therefore, optical path length, mixing intensity, and light distribution influence whether induction affects the bulk culture or only the surface [6,55]. These constraints are consistent with observations of aggregate-driven heterogeneity in *Nostoc* ecology and controlled cultivation [3,6]. Scale-up often favors cultivation designs with short optical paths and high surface-to-volume ratios rather than deep ponds or large-diameter tubes [50]. Examples include flat-panel or narrow-tube photobioreactors and air-lift systems, which improve light exposure in dense cultures and reduce localized photobleaching [23,30,55].

An example supporting the two-step approach comes from studies on *N. flagelliforme*, which have shown that continuous monochromatic light promotes pigment-specific responses but reduces the total biomass compared to broader spectra [5,49]. To address this, a two-stage lighting strategy was used: cultures were first grown under white light for 9 days to build dense biomass and shifted to a defined red/blue/green mixture for another 9 days. This approach improved final biomass and extracellular matrix production compared to static light regimens [6]. This approach is commercially relevant because cyanobacterial PC is widely used as a natural colorant and nutraceutical/cosmeceutical ingredient produced through mass cultivation, extraction, and purification. Although commercial spirulina, genus *Limnospira*, and former *Arthrospira* currently dominate the market, studies on *Nostoc* suggest that light-regime optimization using controlled LED lighting could improve *Nostoc* productivity as an alternative producer [6,14,21,26,58]. Proper design is important, as dense *Nostoc* cultures can self-shade, and targeted induction, such as red light for PC or UV-A for scytonemin, must be balanced against biomass loss. Overall, these findings support the use of two-step cultivation to separate biomass accumulation from stress-induced pigment synthesis, improving productivity in *Nostoc* cultivation systems.

6. Effects of Environmental Stress, Climate Change, and Scale-Up Challenges

Although monochromatic light can induce specific pigment responses, mixed wavelengths often support better overall performance, especially when the goal is to balance biomass formation with product accumulation. For example, when culturing *N. flagelliforme*, a “wavelength-shift” strategy—white light followed by a switch to a red:green:blue mixture (12:5:5)—significantly increased biomass and extracellular polysaccharide production [6]. However, the effects of light on *Nostoc* pigment biosynthesis do not occur in isolation and are influenced by environmental and cultivation factors that alter cellular redox balance,

energy and nutrient utilization, and the effective light intensity experienced by cells in the colony. In this context, spectrum determines photon absorption, intensity regulates the excitation pressure and photodamage risk, and photoperiod controls recovery and repair capacity, influencing the pigment composition and productivity [1,23]. Cross-study comparisons are limited by differences in lighting technology and reporting, including light spectra, culture depth, and PPFD measurement, which may make it difficult to distinguish true biological variation among strains. Therefore, reporting spectrum, PPFD, photoperiod, culture depth, and system design are essential for distinguishing the technical effects from biological responses.

Nutrient availability (especially nitrogen) shifts the balance between growth and pigment/protective systems, and stress can strengthen or induce spectrum-driven responses [39,44,48]. This is important because PBPs function both as light-harvesting pigments and as internal nitrogen reserves; under nitrogen limitation, cyanobacteria mobilize these proteins, leading to bleaching and a reduced PBP content regardless of the light spectrum [14,43]. Therefore, nitrogen supply should be considered with light optimization. As both pigment biosynthesis and nitrogen fixation (via nitrogenase) are energy-intensive, pigment induction under high light or UV can compete for ATP and reducing power, particularly in heterocyst-forming strains; therefore, optimization should consider nitrogen status and nitrogen fixation performance, where relevant [1,14]. Salinity, temperature, heavy metals, and general stress physiology interact with light responses, often enhancing carotenoid-based photoprotection and destabilizing PBPs under harsh conditions [4,35,52]. In *N. muscorum*, for instance, combined salt stress and UV-B caused a stronger reduction in PC and Chl *a* than either stressor alone, despite the upregulation of antioxidant enzymes [59]. Under severe light or UV stress, *Nostoc* may shift its energy to protective pigments (e.g., carotenoids and scytonemin), and strong UV-B rapidly suppresses nitrogenase activity, indicating that survival can take priority over nitrogen fixation [25,39]. Moreover, the effects of the light spectrum also depend on irradiance. Moderate intensities promote CCA, whereas excessive irradiance may shift cells to generalized stress responses, including carotenoid and scytonemin production [11,37].

Temperature also plays a critical role. Low temperatures combined with light stress induce specific alterations in fatty acid and pigment profiles as a survival mechanism [46], whereas high temperatures (e.g., 39 °C) mimic the physiological effects of green light, altering the PE:PC ratio, even under white light [12]. High temperatures induce pigment ratio shifts similar to those triggered by specific light colors, although its mechanistic link to chromatic acclimation signaling remains unclear and may involve redox/ROS signaling [1]. Furthermore, the toxicity of heavy metals such as chromium (Cr VI) in *N. commune* has been shown to be wavelength-dependent, with specific light spectra influencing the photochemical efficiency of PSII under metal stress conditions [36]. Cultivation is also crucial, as *Nostoc* often grows as colonies, mats, or aggregates, in which self-shading and diffusion limits create internal gradients in intensity and spectrum, leading to heterogeneous pigment accumulation that cannot be predicted from incident light alone [3,8,55]. In addition, strain and species differences, which are shaped by habitat history (e.g., terrestrial/desiccation-exposed forms), influence sheath development and thus scytonemin potential and UV tolerance [3,10,47]. The photoperiod influences tolerance to spectrum–intensity combinations because dark phases enable PSII repair and PBP recovery after high light exposure [48,54]. These factors are expected to become even more important given climate change.

Climate change is an increasingly important factor to consider because it alters the light and stress conditions experienced by *Nostoc* species. Warmer temperatures and more frequent droughts can intensify desiccation, reduce water films, and expose colonies and

mats to stronger sunlight and UV, especially in terrestrial habitats, increasing the risk of severe cellular damage [3,8,10]. Under continuous stress, *Nostoc* may produce more protective pigments and fewer light-harvesting pigments; thus, shifts in colony color reflect changes in photosynthetic performance and stress tolerance [35,44,48]. To survive intense drying, species such as *N. flagelliforme* produce specialized “red proteins” (HCPs) that act as safety valves, binding carotenoids and dissipating excess absorbed light as heat when water is unavailable for normal photosynthesis [19,46]. Extreme temperatures alone can also modify the organization and pigment ratios of the light-harvesting apparatus [12,46]. A major challenge is adapting laboratory light strategies to outdoor or industrial cultivation, as *Nostoc* experiences fluctuating sunlight, self-shading, and multiple stressors. LED supplementation and two-stage induction may stabilize pigment production on larger scales.

Despite recent progress, several key knowledge gaps must be addressed to make light-driven pigment optimization in *Nostoc* scalable and predictive. The pigment composition varies among strains and is influenced by environmental factors, suggesting that strain-specific responses should be considered when developing optimization strategies for *Nostoc* [40,42,58]. Moreover, studies on scytonemin have explained induction and function, but few report production-ready parameters under controlled UV-A/UV-B dosing conditions [25,46,47,53]. Scale-up is also challenging because colonies and mats create strong internal light gradients (self-shading); thus, incident PPFD alone may not predict pigment outcomes [3,8,55]. Future work should optimize biomass and pigment productivity together (not pigment percentage alone) and connect cultivation conditions to downstream pigment stability and processing performance. Additional priorities include standardized LED studies with full spectral reporting, volumetric pigment productivity, scale-up design and mixing, and stress indicators, such as ROS-related responses, Chl *a* stability, and pigment changes.

7. Conclusions

Pigment production in *Nostoc* species is strongly regulated by the light environment, making light regulation a key strategy for pigment optimization. Production systems should move beyond static white light and use dynamic LED lighting designed for specific pigment targets. PBPs are governed by chromatic adaptation, and moderate red light favors PC productivity, whereas green-enriched light promotes PE accumulation in responsive strains. In contrast, high light and UV exposure should be used as short induction treatments for protective pigments, such as carotenoids and scytonemin, as prolonged stress can reduce biomass productivity. Pigment responses cannot be interpreted from light spectrum alone. Studies should report spectral composition, PPFD, photoperiod, and cultivation system design to improve comparability. Environmental factors, such as temperature, nutrient availability, salinity, and climate-related stress, also interact with light responses and should be integrated into optimization studies. Overall, optimized lighting conditions, two-stage cultivation, and improved process design may transform *Nostoc* into a scalable system for high-value pigment production.

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Abbreviations

The following abbreviations are used in this manuscript:

UV	Ultraviolet
Chl <i>a</i>	Chlorophyll <i>a</i>
PBPs	Phycobiliproteins
PC	Phycocyanin
PE	Phycocerythrin
APC	Allophycocyanin
PBS	Phycobilisomes
PSI	Photosystem I
PSII	Photosystem II
ROS	Reactive oxygen species
HCPs	Helical carotenoid proteins
OCP	Orange carotenoid protein
CCA	Complementary chromatic adaptation
Rca	Regulator of chromatic adaptation
CBCRs	Cyanobacteriochromes
PPFD	Photosynthetic photon flux density
EPS	Extracellular polymeric substances
MAAs	Mycosporine-like amino acids
PAR	Photosynthetically active radiation

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