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UV-B-Induced Synthesis of Photoprotective Pigments and Extracellular Polysaccharides in the Terrestrial Cyanobacterium *Nostoc commune*

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Liquid cultures of the terrestrial cyanobacterium *Nostoc commune* derived from field material were treated with artificial UV-B and UV-A irradiation. We studied the induction of various pigments which are thought to provide protection against damaging UV-B irradiation. First, UV-B irradiation induced an increase in carotenoids, especially echinenone and myxoxanthophyll, but did not influence production of chlorophyll *a*. Second, an increase of an extracellular, water-soluble UV-A/B-absorbing mycosporine occurred, which was associated with extracellular glycan synthesis. Finally, synthesis of scytonemin, a lipid-soluble, extracellular pigment known to function as a UV-A sunscreen, was observed. After long-time exposure, the UV-B effect on carotenoid and scytonemin synthesis ceased whereas the mycosporine content remained constantly high. The UV-B sunscreen mycosporine is exclusively induced by UV-B (<315 nm). The UV-A sunscreen scytonemin is induced only slightly by UV-B (<315 nm), very strongly by near UV-A (350 to 400 nm), and not at all by far UV-A (320 to 350 nm). These results may indicate that the syntheses of these UV sunscreens are triggered by different UV photoreceptors.

The terrestrial nitrogen-fixing cyanobacterium *Nostoc commune* Vaucher flourishes in extremely cold and dry habitats which are characterized by intense solar radiation, extreme temperature differences, and regular periods of desiccation (34, 42; for a review, see reference 7). *N. commune*, in its natural habitat, forms macroscopic colonies with filaments embedded in gelatinous glycan. In the past, most studies concentrated on the extraordinary drought resistance of *N. commune* (33; for a review, see reference 29), but only few investigated its UV tolerance (35, 41).

Mechanisms counteracting UV-B damage have been demonstrated in plants and cyanobacteria. Besides repair of UV-induced damages of DNA by excision repair and photoreactivation (10, 26) and accumulation of detoxifying enzymes and carotenoids (24, 25), an important mechanism to prevent UV photodamage is the synthesis of UV-absorbing compounds. Several studies provide evidence that epidermally located phenylpropanoids, especially flavonoid derivatives, protect higher plants by absorbing harmful UV radiation (22, 37). Mycosporine amino acids (MAAs) are thought to fulfill a comparable purpose in lower organisms (14, 21). MAAs are water-soluble, substituted cyclohexenes which are linked to amino acids and iminoalcohols and have absorption maxima between 310 and 360 nm. Scytonemin, which has an in vivo absorption maximum at 370 nm and is located in the cyanobacterial sheath, has been proposed to serve as a UV-A sunscreen (13). It is a yellow-brown, lipid-soluble dimeric pigment of terrestrial cyanobacteria with a molecular mass of 544 Da and a structure based on indolic and phenolic subunits (30).

A UV-A/B-absorbing pigment with absorption maxima at 312 and 335 nm was found in *N. commune* colonies exposed to high solar radiation (35). Recently, its chemical structure has been shown to be an oligosaccharide MAA (OS-MAA) (1). It was the first mycosporine reported to be covalently linked to oligosaccharides and is located in the extracellular glycan, where it forms high-molecular-weight complexes which are attached to the cyanobacterial sheath by noncovalent interactions (1, 16). Because *N. commune* is subject to regular cycles of desiccation and rewetting and often must survive long periods in quiescence, during which repair mechanisms are ineffective, UV-absorbing compounds may play a key role in UV photoprotection of *N. commune.*

The aim of this work was to study, in a single organism, the sequence of UV-induced synthesis of carotenoids, scytonemin, and a mycosporine, which are suggested to provide protection against UV damage.

MATERIALS AND METHODS

Organism and growth conditions. The cyanobacterium *N. commune* Vaucher DRH1 (hereafter referred to *N. commune* DRH1) was derived from field material of *N. commune* collected in Hunan province, People's Republic of China (17). The strain grows in liquid media under laboratory conditions without producing a visible glycan sheath surrounding single filaments. For UV induction experiments, 50 ml of *N. commune* DRH1 liquid cultures was grown under nitrogen-fixing conditions at 30°C in a 200-ml flask in $BG11_0$ (32) medium with constant shaking (80 rpm) to avoid self-shading. The flasks (Duran; Schott, Mainz, Germany) function as UV-C filters. The cultures were illuminated from above. Visible light (ca. 2.4 W m^{-2}) was obtained from a cool white fluorescent tube (L40W/25 S, Osram, Munich, Germany). Additional illumination was provided from a Philips TL40W/12 lamp with incident irradiances of 100 to 140 mW m^{-2} nm^{-1} at 310 nm and 50 to 70 mW m^{-2} nm^{-1} at 330 nm. UV-A control experiments were performed with a Philips TL36W/08 lamp with an emission maximum centered at 375 nm. Foils with a cutoff at 315 nm were used as UV-B-blocking filters. The spectral irradiance which was received by the cultures after passing the flask and filters is presented in Fig. 1. Since no measurements are available, the maximum values of incident solar UV-B radiation in the natural habitat of *N. commune* DRH1 were calculated by the method of Feister (11) to vary between 0.7 W m^{-2} (winter) and 2 W m^{-2} (summer), around noon and on cloudless days. The UV-B irradiation applied in our experimental setting was 1 W m^{-2}.

Photon flux density in the visible spectral region was measured with a photodiode (G1118; Hamamatsu Photonics K. K., Hamamatsu, Japan), which was

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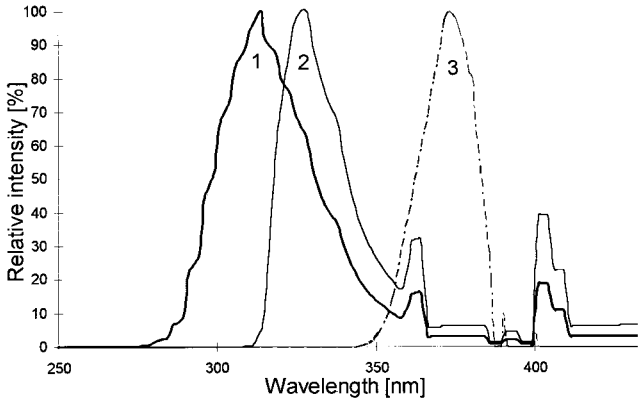

FIG. 1. Comparison of the spectral characteristics of UV light received by cultures in flasks from different light sources and filters. Curves: 1, lamp TL-12 (UV-B plus far UV-A; λ_{max} = 315 nm, ca. 1.0 W of UV-B m^{-2} plus 0.6 W of UV-A m^{-2}); 2, lamp TL-12 plus 315-nm cutoff filter (far UV-A only, λ_{max} = 330 nm, ca. 0.5 or 1.0 W m^{-2}); 3, lamp TL-08 (near UV-A, λ_{max} = 375 nm, ca. 1.7 W m^{-2}).

calibrated with an Osram L40W/25 S lamp against a quantumsensor (LI-190B; Li-Cor, Lincoln, Neb.). UV radiation was measured with a UV-B sensor (UV-S-310-C; Scintec, Tübingen, Germany) calibrated by the manufacturer with a Philips TL40W/12 lamp as the light source.

Growth measurements. Cultures were sampled under sterile conditions at indicated intervals and homogenized with a motor-driven tissue grinder (Glas-Col, Terra Haute, Ind.) rotating at 500 rpm. Cell number was determined by cell counting of 1:2 dilution series in a hemocytometer (Neubauer Chamber; Brand, Wertheim, Germany). Dry weight was determined gravimetically after desiccation at 85°C overnight and room temperature equilibration under $CaSO_4$.

Extraction of pigments. For extraction of carotenoids and scytonemin, cells were harvested by centrifugation and concentrated under vacuum to remove the remaining water. Samples were extracted with 100% acetone by grinding the cells in the solvent with a motor-driven tissue grinder (Glas-Col), rotating at about 1,500 rpm, under nitrogen in darkness. Extracts were clarified by centrifugation. Samples for the carotenoid composition determination were stored under nitrogen at −70°C in darkness until high-pressure liquid chromatography (HPLC) analysis was performed. For extraction of OS-MAA, samples were extracted in 30% methanol (30 min at 50°C) or in 100% methanol (30 min at 60°C) in darkness as described by Scherer et al. (35) and clarified by centrifugation.

Determination of pigment contents. UV-visible spectra were obtained with an Ultraspec 2000 photometer (Pharmacia Biotech, Uppsala, Sweden) immediately after extraction of the pigments. Scytonemin, chlorophyll *a*, and total carotenoids were quantified from the recorded spectra of acetone extracts by using a set of trichromatic equations (12). Specific extinction coefficients used were 92.60 liters g^{-1} cm^{-1} at 663 nm for chlorophyll *a* (40), 112.6 liters g^{-1} cm^{-1} at 384 nm for scytonemin (13), and 250 liters g^{-1} cm^{-1} at 490 nm for total carotenoids (2). The OS-MAA content was calculated from recorded spectra of the 30% methanol extracts by using a specific extinction coefficient of 17 liters g^{-1} cm^{-1} at 312 nm (1).

Carotenoid composition was analyzed using reversed-phase HPLC (RP-HPLC) (Hypersil ODS 5 μ column, 250 by 4.6 nm; Alltech Associates Inc., Deerfield, Ill.). For details of the system used, see reference 23. Before injection, the 100% acetone extracts were diluted with water to 80% acetone. Solvent A consisted of 35% acetone, 52% methanol, and 13% water (vol/vol/vol); solvent B consisted of 100% acetone. Chromatography was started with 100% solvent A for 8.5 min and changed in a linear gradient to 69:31 (vol/vol) solvent A/solvent B within 30 s. After running isocratically at this composition for 3.5 min, the composition was changed in a linear gradient to 30:70 (vol/vol) solvent A/solvent B within 14 min, followed by a linear change to 100% solvent B within 30 s. After 2 min at 100% solvent B, the system was returned to the initial conditions and was equilibrated for 9 min. Carotenoids were identified and calibrated by using standards {zeaxanthin [(3R,3′R)-β,β-carotene-3,3′-diol] and canthaxanthin [β,β-carotene-4,4′-dione] from Roth, Karlsruhe, Germany; β-carotene from Sigma, Deisenhofen, Germany; and echinenone [β,β-carotene-4-one], an isolate donated by F.-C. Czygan, Würzburg, Germany}. Myxoxanthophyll [myxol-2′-rhamnoside or 2′-(β-L-rhamnopyranosyloxy)3′,4′-didehydro-1′,2′-dihydro-β,ψ-carotene-3,1′-diol] was tentatively identified by comparing retention time and on-line absorbance spectra with published values (5). Other carotenoids were not detected. However, in *Nostoc* sp. strain Bu94.1, which was isolated by B. Büdel, Rostock, Germany, from the lichen *Peltigera rufescens* (Weis) Humb., two further carotenoids could be separated and were tentatively identified as myxol-2′-*o*-methyl-methylpentoside and 4-keto-myxol-2′-rhamnoside by using the same chromatography system (43). Chlorophyll *a* was calibrated by using an extract of *Synechococcus* sp.

All experiments described were conducted independently at least twice with three replicates each, the mean values given in Results representing averages of six assays. Mean separation was based on the calculation of 95% confidence limits from the appropriate experimental error mean square and tabulated *t* value.

RESULTS

General growth response upon UV irradiation. Short-time exposure to UV-B for 1 or 1.5 days had negligible effects on the growth of *N. commune* DRH1. No significant differences ($P < 0.05$) in cell number, dry weight, or chlorophyll *a* content were observed (Table 1). Prolonged UV-B exposure led to a decrease of cell replication by about 60% and, simultaneously, two- to threefold-increased dry weight per cell compared to control cultures (Table 1). Light microscopic observation showed that UV-B irradiation induced synthesis of sheath material surrounding the filaments (Fig. 2). The sheath can be visualized by negative staining with 1% nigrosin and was absent around single filaments in control cultures (data not shown). The yield of a large-scale glycan isolated from UV-B-irradiated cultures was about three times higher than that from control cultures (data not shown), indicating that the dry weight increase upon UV-B radiation can be essentially attributed to a stimulated extracellular glycan production.

The UV-B-dependent induction of pigments occurred in three phases, involving carotenoids, mycosporine, and scytonemin. Because chlorophyll *a* content per cell remained unaffected even after prolonged exposure to UV-B, while total dry weight was rising (Table 1), all pigment contents are given relative to that of chlorophyll *a*.

Induction of carotenoids. After 5 h of UV-B treatment at 1.0 W m^{-2}, a first significant increase of total carotenoids was observed (data not shown). The total carotenoid-to-chlorophyll *a* ratio after 1 day of UV-B irradiation was 34 to 40% higher than the control value (Fig. 3A). After 5.5 days of UV-B

TABLE 1. Growth response of *N. commune* DRH1 cultures upon UV-B irradiation[a]

Exposure time (days)	Mean ± SD					
	Cell no. (10^7 cells/ml)		Chl *a* (μg/10^7 cells)[b]		Dry wt (μg/10^7 cells)	
	Control	+UV-B	Control	+UV-B	Control	+UV-B
1	2.2 ± 0.5	2.5 ± 0.5	1.7 ± 0.4	1.5 ± 0.4	ND[c]	ND
6.5	9.3 ± 0.7	3.9 ± 0.4	1.1 ± 0.2	1.4 ± 0.2	150 ± 20	370 ± 50

[a] DRH1 was cultivated at 30°C with cold fluorescent light of 2.4 W m^{-2} and artificial UV-B irradiation of 1.0 W m^{-2} (emission spectrum 1 [Fig. 1]). The control culture received the same intensity of fluorescent light without UV-B.
[b] No significant differences were detected ($P < 0.05$). Chl *a*, chlorophyll *a*.
[c] ND, not determined.

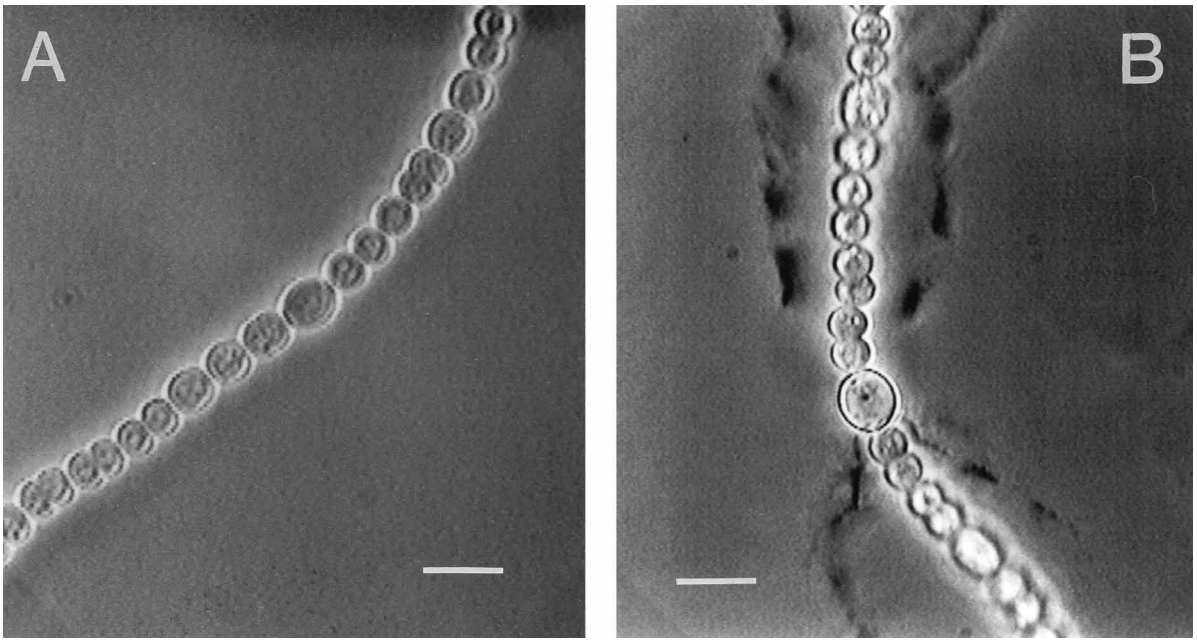

FIG. 2. *N. commune* DRH1 filaments grown in liquid culture; unstained light microscopic picture. (A) Typical appearance of *N. commune* DRH1 grown in liquid culture without UV-B; (B) DRH1 liquid culture after 72 h of UV-B irradiation (1.0 W m^{-2}). Note that glycan is absent around heterocysts. Bars indicate 10 μm.

exposure, the enhanced carotenoid-to-chlorophyll *a* ratio declined to about 115% compared to controls.

To analyze whether UV-B led to a general shift-up in all carotenoids or whether specific carotenoids were induced, carotenoid patterns were analyzed by RP-HPLC. Figure 3B shows the carotenoid pattern of *N. commune* DRH1 after 1 day of UV-B treatment and the corresponding pattern of the control culture. As reported for other cyanobacteria (15), the carotenoid composition of *N. commune* was dominated by β-carotene, echinenone, and myxoxanthophyll, while canthaxanthin and zeaxanthin were only minor components. Specific contents (milligrams of pigment/milligram of chlorophyll *a*) of echinenone, myxoxanthophyll, and canthaxanthin were significantly increased ($P < 0.01$), while β-carotene and zeaxanthin showed no significant differences in comparison to control cultures. No additional carotenoids were induced by UV-B irradiation. The carotenoids mainly affected by UV-B were echinenone and myxoxanthophyll. Their specific content increased about 40 to 50% in comparison to control cultures.

The induction of carotenoids was due to UV-B, since filters with a cutoff at 315 nm (Fig. 1) prevented an increase in carotenoids (Table 2). Cultures irradiated with near UV-A (λ_{max} = 375 nm) also showed an increase in carotenoid-to-chlorophyll *a* ratios, but the induction followed completely different kinetics because carotenoids increased continuously over five days (Table 2).

Induction of mycosporines. UV-B exposure led to the production of UV-A/B-absorbing OS-MAA with absorption maxima at 312 and 335 nm (Fig. 4). The total amount of OS-MAA per milliliter of culture increased during the entire UV-B exposure time, but the specific content rose to a maximum of about 4.5 mg per mg of chlorophyll *a* at 3.5 days and remained at this high value (Fig. 5A). Synthesis of the pigment was promoted neither by supplemented UV-A irradiation (Table 2) nor by other stresses such as increased temperature, desiccation, or salt (data not shown). Traces of OS-MAA could be detected in old control cultures not subjected to UV stress.

Induction of scytonemin. No scytonemin was detected in control cultures grown without UV. UV-B irradiation induced scytonemin production after an initial lag of about 1 day. The specific content rose to a maximum of about 0.38 mg/mg of chlorophyll *a* at 2.5 days and declined thereafter (Fig. 5B). The induction of scytonemin was mostly due to the UV-B part (λ_{max} = 315 nm) emitted by the UV-B light source, because cultures protected by filters with a cutoff at 315 nm (far-UV-A irradiation, λ_{max} = 330 nm) showed only a very low scytonemin production of about 6% compared to unfiltered cultures (Table 2). Even higher far-UV-A irradiations led to only very low scytonemin production, whereas near-UV-A irradiation (λ_{max} = 375 nm) induced scytonemin production two- to threefold in comparison to cultures treated with UV-B (Table 2).

DISCUSSION

Synthesis of extracellular polysaccharides is induced by UV-B. Long-time UV-B, but not UV-A, exposure of *N. commune* DRH1 led to a decreased cell number but increased dry weight in comparison to control cultures, while short-time UV-B exposure had negligible effects on the growth of *N. commune* (Table 1). We suggest that the decreased cell number observed after 6 days of UV-B exposure is due to a slower cell replication caused by the metabolic cost of increased glycan production and is not a consequence of inhibition of cell replication by UV-B. To our knowledge, the influence of UV-B on extracellular glycan production had not previously been studied. Since the UV-absorbing mycosporines induced simultaneously are located in the glycan sheath (1, 35), it is likely that an increased glycan production serves to provide a matrix for the OS-MAA, which is closely attached to the glycan by noncovalent interactions (1, 16). A thicker sheath provides much longer effective path lengths for the absorption of radiation. Whether UV-B led to structural changes of exopolysaccharides is currently under investigation.

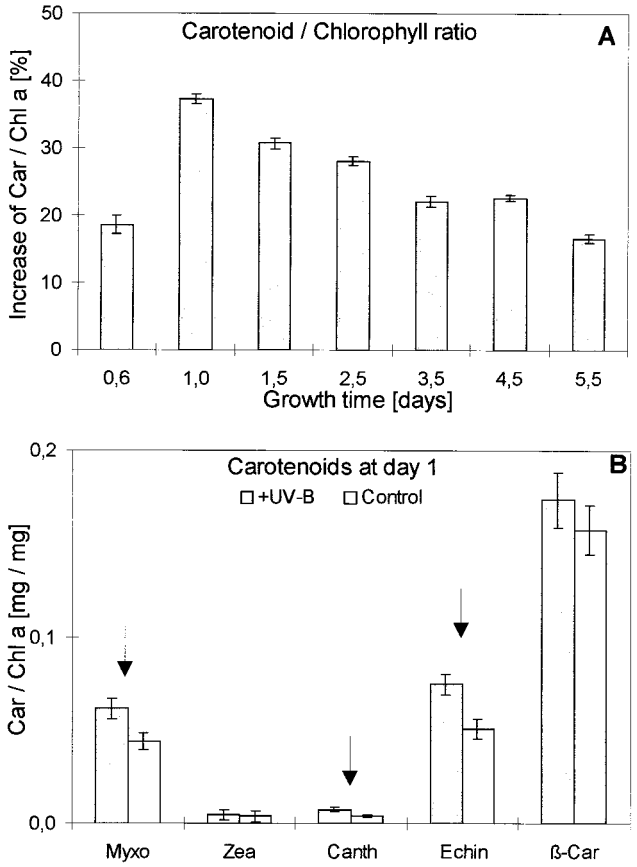

FIG. 3. Influence of UV-B irradiation on carotenoid synthesis. (A) Changes in total carotenoid/chlorophyll *a* (Car/Chl a) ratios in response to UV-B irradiation of 1.0 W m^{-2}. Values for UV-exposed cells were calculated and compared with those for non-UV-exposed cells and presented as mean percentage increase ($P < 0.05$) ± standard error. (B) Changes in carotenoid patterns after 1 day of UV-B irradiation monitored by RP-HPLC. Stippled bars, UV-B irradiation; white bars, controls. Abbreviations: Myxo, myxoxanthophyll; Zea, zeaxanthin; Canth, canthaxanthin; Echin, echinenone; β-Car, β-carotene. ↓ denotes significantly different values compared to the control ($P < 0.05$).

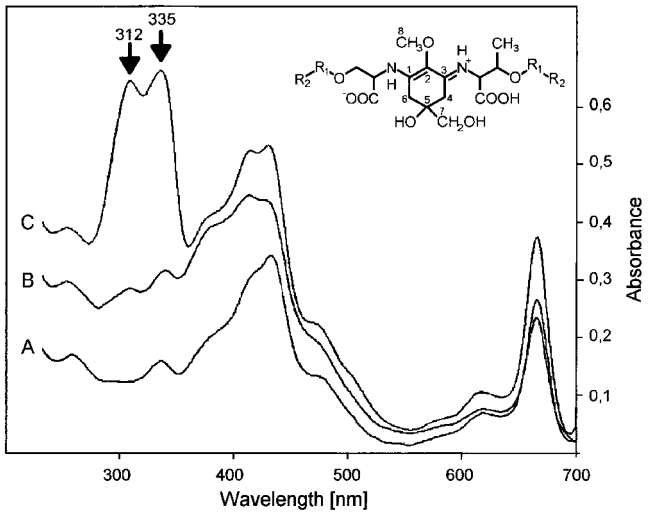

FIG. 4. Absorption spectra of DRH1 in 100% methanol. A, before UV-B treatment; B, 1 day of UV-B irradiation; C, 5.5 days of UV-B irradiation. Inset: structure of the 335-nm chromophore according to Böhm et al. (1). R1, galactose, xylose, and glucuronic acid; R2, galactose, glucose, and glucosamine.

Myxoxanthophyll and echinenone could be envelope membrane-bound UV photoprotectors. For photosynthetic organisms, the protective role of carotenoids against high visible radiation is well known (36; for a review, see reference 6), and a protective role of carotenoids in cyanobacteria against UV-A radiation was reported (3, 28). Only little is known about the role of carotenoids in photoprotection against UV-B radiation (24, 31). Cyanobacteria produce some unique types of xanthophylls, such as ketocarotenoids and glycosides (18). Interestingly, in *N. commune* DRH1, these unique types were induced by UV-B whereas β-carotene and zeaxanthin showed no response (Fig. 3B). Analysis of cyanobacterial envelope membranes demonstrated that xanthophylls are the predominant carotenoids, whereas β-carotene was found almost exclusively in the thylakoids (20, 27). Myxoxanthophyll, a pigment induced by UV-B in *N. commune* DRH1 (Fig. 5B), has been shown to be the predominant pigment in the outer membrane of *Synechocystis* sp. strain PCC 6714 (19). Echinenone, the other carotenoid strongly induced by UV-B in *N. commune* DRH1 (Fig. 5B), has also been found in the outer membrane of *Synechocystis*, but only as a minor compound. The function of the carotenoids in outer membranes of cyanobacteria is still not clear. Since it has been shown that heterologous expression of carotenoid genes in *Escherichia coli* led to an increased resistance to UV radiation (38, 39), our results suggest that myxoxanthophyll and echinenone may, indeed, act as outer membrane-bound UV-B photoprotectors of *N. commune*. They may be induced as a fast, SOS-type response before extracellular UV sunscreens can be synthesized.

TABLE 2. Wavelength dependence of pigment induction[a]

Time (days)	Mean ± SD								
	Car/Chl *a* (% increase)			OS-MAA-Chl *a* (mg/mg)			Scyt/Chl *a* (mg/mg)		
	Far UV-A + UV-B[b]	Far UV-A only[c]	Near UV-A[d]	Far UV-A + UV-B	Far UV-A only	Near UV-A	Far UV-A + UV-B	Far UV-A only	Near UV-A
1	37.3 ± 0.7	3.1 ± 0.5	26.2 ± 0.9	2.0 ± 0.3	—	—	0.05 ± 0.02	—	ND
2.5	28.1 ± 0.7	5.2 ± 0.6 (10.9 ± 0.7)	30.3 ± 0.7	3.6 ± 0.5	— —	—	0.38 ± 0.03	0.02 ± 0.01 (0.03 ± 0.01)	1.1 ± 0.04
4.5	22.6 ± 0.4	0.2 ± 0.4	45.3 ± 0.5	4.6 ± 0.4	—	—	0.23 ± 0.05	—	ND

[a] Car, total carotenoids; Chl *a*, chlorophyll *a*; scyt, scytonemin, ND, not determined, —, not detected. DRH1 cultures received visible light (about 2.4 W m^{-2}) supplemented with following UV irradiations as indicated in footnotes *b* to *d*. For detailed spectrum characteristics of UV treatments, see Fig. 1.
[b] λ_{max} = 315 nm, ca. 1.6 W m^{-2}.
[c] λ_{max} = 330 nm, ca. 0.5 W m^{-2} (or 1.0 W m^{-2}).
[d] λ_{max} = 375 nm, ca. 1.7 W m^{-2}.

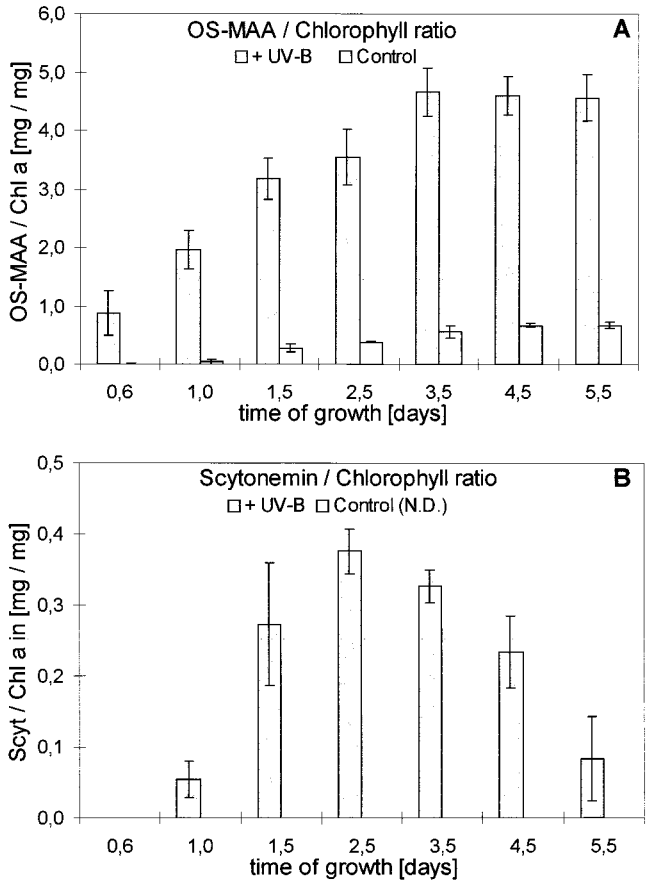

FIG. 5. UV-B-induced synthesis of extracellular UV-absorbing compounds in liquid cultures of DRH1. Shown are time courses of oligosaccharide-MAA (A) and scytonemin (Scyt; B) contents at 1.0 W of UV-B m^{-2}. Stippled bars, UV-B irradiation; white bars, controls. Error bars denote standard deviations of means. N.D., not detected. Chl a, chlorophyll *a*.

UV-B induced the synthesis of two extracellular sunscreen pigments. UV-B irradiation of *N. commune* DRH1 led to the production of the water-soluble UV-A/B-absorbing pigment, which belongs to the group of MAAs, and the production of the lipid-soluble scytonemin (Fig. 5). However, the scytonemin content of UV-B-treated cultures was 1 order of magnitude less than OS-MAA content. MAAs may play an important role in photoprotection of *N. commune* because the OS-MAA is located in the extracellular glycan. The pigment provides protection, mainly by absorbing the harmful radiation, but the 312-nm chromophore of the pigment, which is thought to be a MAA-Gly (1), may provide additional protection by radical quenching (8). No photobleaching of chlorophyll *a* was observed in OS-MAA-producing *N. commune* DRH1 upon UV-B irradiation (Table 1), whereas *Nostoc* sp. strain Bu94.1, which produces scytonemin but no MAAs, completely bleached when it was treated with UV-B (9).

UV-B-irradiated liquid cultures of *N. commune* contained about 2% OS-MAA by dry weight (this study). Amounts of OS-MAA found in desiccated field material (35), estimated by using the same extinction coefficient, correlate well with this value. As both OS-MAA and glycan syntheses increased due to UV-B, but not in response to UV-A, some correlation of extracellular polysaccharide and OS-MAA induction may exist. UV-A- and UV-B-induced syntheses of scytonemin in *N. commune* DRH1 followed similar kinetics, but pigment concentrations in UV-B-treated cultures were only about 30% of those of UV-A-treated cultures.

We propose that OS-MAA is the key pigment in UV-B protection whereas scytonemin is most effective in UV-A protection. However, the latter may have some special role as a UV-B protectant immediately after rewetting of desiccated colonies. In contrast to OS-MAA, scytonemin is not lost upon rewetting. Since it has some absorption in the UV-B range, it may provide some protection against UV-B in MAA-depleted field material.

Potential UV photoreceptors. Our results suggest that OS-MAA synthesis and scytonemin synthesis may be regulated by different photoreceptors. The synthesis of OS-MAA is induced by a UV-B photoreceptor absorbing at wavelengths below 315 nm (Table 2). A separate UV-A photoreceptor probably regulates scytonemin because its synthesis is most pronounced at near-UV-A (350- to 400-nm) irradiation, whereas far-UV-A (320- to 350-nm) irradiation had little effect. In addition to the induction by UV-A, there is a slight induction of scytonemin by UV-B (Table 2). UV-B induction and UV-A induction of chalcone synthetase are regulated separately (4). Based on our data, however, it is not possible to assess the small effects of UV-B on scytonemin.

Conclusion. Photon fluence rates of UV-B which are within the magnitude of solar fluence rates induce a cascade of physiological reactions in *N. commune*. In its natural habitat, *Nostoc* has to cope with high solar radiation in its dry state, in which photodamage cannot be efficiently repaired. Therefore, passive photoprotective mechanisms are needed. The water-soluble OS-MAA provides passive protection against UV-B and far-UV-A irradiation (1), whereas the lipid-soluble scytonemin, beside some absorption in the UV-B range, absorbs mainly UV-A (12). Since carotenoid synthesis is induced very quickly upon UV-B irradiation, outer membrane-bound carotenoids may play a role in photoprotection immediately after rewetting of desiccated colonies when the OS-MAA content is low. We propose that carotenoids, in UV protection, provide a fast, active SOS response to counteract acute cell damage whereas the extracellular glycan with its UV-absorbing pigments is a passive UV screen against long-time exposure.

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