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Research article

Ecological screening and functional analysis of pigments, antioxidants and potent sunscreen compounds in cyanobacteria inhabiting diverse habitats

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Abstract: Cyanobacteria are incredibly versatile and morphologically the most diverse prokaryotic organisms across the globe. Cyanobacteria are capable of synthesizing their own protective metabolites in any harsh environmental condition. Moreover, anthropogenic-induced depletion of the ozone layer has consistently increased UV radiation intensity on the Earth surface. In response to solar radiation, cyanobacteria synthesize photoprotective compounds, including mycosporine-like amino acids (MAAs), which provide active protection against solar radiation. In this study, cyanobacteria from diverse habitats, including rice-fields, hot-springs, monuments, rocks, and tree barks, were sampled and isolated. A total of nine cyanobacteria were selected from habitats which have shown different pigment compositions (Chl *a*, carotenoids, and PBPs), and enzymatic (SOD, POD, and CAT) antioxidant profiles based on their native habitats. The non-enzymatic UV-absorbing pigment, MAAs, were extracted using 100% methanol and partially purified through high-performance liquid chromatography (HPLC). The preliminary acquired data revealed that screened MAAs were MAAs-334 (λ_{max} = 334 nm), MAAs-310a, b (λ_{max} = 310 nm), MAAs-331 (λ_{max} = 331 nm), MAAs-320a, b, c, d (λ_{max} = 320), MAAs-321 (λ_{max} = 321), and MAAs-322 (λ_{max} = 322 nm). In addition, six peaks (λ_{max} = 275, 277, 290, 296, 313, 319 nm) were detected. These results were utilized for isolation of novel MAAs and advancement of production at a large scale from diverse habitats of cyanobacteria. Furthermore, UV-absorbing MAAs may have future potential for application in sunscreen formulations.

Keywords: antioxidant; cyanobacteria; high-performance liquid chromatography; mycosporine-like amino acids; UV radiation

1. Introduction

The stratospheric ozone layer depletion over the course of the last four decades has resulted with the increase in ultraviolet (UV-B) radiation, reaching the surface of our green planet [1]. Strong UV-B radiation is thought to be extremely detrimental to living things, causing acute and chronic dermatological disorders, DNA alterations, reactive oxygen species (ROS) explosions, stunted development, and death [2]. It is generally recognized that mycosporine-like amino acids (MAAs) act as strong photoprotectants by reducing photo-induced ROS production as well as dissipating extra energy in the form of heat [3]. These photoprotectants are a group of low molecular-weight (188 to 1050 Da), water-soluble, UV-absorbing compounds. The structural backbone of MAAs consists of either cyclohexenone or cyclohexeniminone rings with substitution of nitrogen and mono or di-amino acids [4]. The wide variety of MAAs differ in their absorption maxima, ranging from 310 to 360 nm and molar absorptivity (2.81×10^4 to 5.00×10^4 $M^{-1}\cdot cm^{-1}$). These characteristics harbor them with beneficial properties such as antioxidants, anti-aging, anti-cancerous, or anti-inflammatory agents, and thermal and UV protectants, which serve to be a promising compound for various applications in the cosmetics sector [2,5]. Indeed, two commercial sunscreen lotions (Helioguard 365 and Helionori) have been marketed using a composition that contains shinorine as an active component. This is an essential step for developing the next generation of sun care formulations [5].

Cyanobacteria are referred as the pioneer living beings on Eath's surface whose fossil records date to 2.4 billion years ago [6]. They are the first prokaryotes capable of performing oxygenic photosynthesis, enabling the emergence of eukaryotic photoautotrophs [7]. The evolutionary persistence of cyanobacteria to date has enabled them to exhibit remarkable taxonomic and ecological diversity [6,8]. The stress resistance is the sole factor for their existence in varied light fluctuations and unavoidable UV rays under natural solar radiation. In concern to harmful UV radiation, cyanobacteria have developed several defense strategies to sustain their survival [9]. One such strategy is to synthesize a variety of MAAs that enable them to withstand UV radiation with the evolving Earth, even before the formation of the ozone barrier [10]. Cyanobacterial species have been shown to synthesize MAAs, which differ in quantity and composition depending on the environmental conditions, such as source and intensity of light, and nutritional constraints [11]. In our experiment, cyanobacteria from diverse habitats (different geographical sites) were used for ecophysiological screening (photopigments and antioxidative enzyme assays) and identification of novel MAAs compounds. The difference in cyanobacterial photosynthetic pigments (especially phycobiliproteins) and MAAs may correspond to their survival adaptation toward their native environment and under direct exposure to solar radiation.

2. Materials and methods

2.1. Geographical site and sample collection

We selected several habitats across four major Indian states, namely Uttar Pradesh (UP), Madhya Pradesh (MP), Haryana, and West Bengal (WB), to collect cyanobacterial samples (Figure 1). In the region of Uttar Pradesh, we selected different geographical sites, such as rice-field habitats of Piparahwa village (24°27'00.5" N 83°09'44.0" E), the monuments and pond ecosystem of Vijaygarh Fort (24°34'36.9" N 83°10'53.4" E) in Sonbhadra, along with soil mat and mango bark inhabitants

from Banaras Hindu University (BHU), Varanasi (25°16'18.7" N 82°59'11.0" E). Furthermore, Sohna, Haryana (28°14'48.5" N 77°03'51.4" E), and Bakreshwar, West Bengal (WB) (23˚52’51” N, 87˚22’30” E), were two sites used to collect hot-spring cyanobacteria. For freshwater cyanobacteria, a moist habitat near the Dudh Dhara Waterfall in the Amarkantak region of Madhya Pradesh (22°42'08.5" N 81°42'08.9" E) was selected.

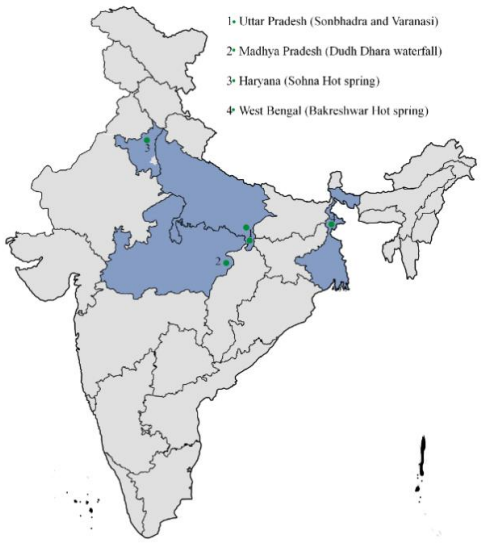

Figure 1. Geographical location of diverse habitats of cyanobacteria. (1) Uttar Pradesh (Sonbhadra and Varanasi), (2) Madhya Pradesh (Dudh Dhara waterfall), (3) Haryana (Sohna, hot-spring), and (4) West Bengal (Bakreshwar, hot-spring).

We also collected physicochemical data, such as temperature and pH, during the collection of cyanobacteria from diverse habitats (Table 1). The selected sampling sites were mostly exposed to solar radiation throughout the year. Photographs were captured using a digital camera of all these sampling sites (Figure 2). Samples were stored in sterile polybags for *in vitro* study.

Table 1. Cyanobacterial collection from diverse habitats of different geographical sites. UP-Uttar Pradesh, BHU-Banaras Hindu University, MP-Madhya Pradesh, and WB-West Bengal.

Geographical sites	Habitats	Physical appearance	pH	Temp. (°C)	Dominant cyanobacteria
Sonbhadra, UP	Rice-field	Bluish-green	6.3–7.2	30 ± 2	*Calothrix* sp. *Anabaena* sp.
	Monuments	Blackish	6.3–7.2	30 ± 2	*Nostoc* sp.
	Pond	Bluish-green	6.8–7.9	30 ± 2	*Aphanothece* sp.
BHU Varanasi, UP	Soil crust	Blackish-green	6.5–7.4	29.4 ± 2	*Oscillatoria* sp.
	Mango bark	Bluish-green	6.5–7.4	29.4 ± 2	*Lyngbya* sp.
Dudh Dhara, Amarkantak, MP	Moist rocky surface	Brownish, bluish-green	6.7–7.3	29.6 ± 2	*Nostoc* sp.
Sohna, Haryana	Hot-spring	Blackish, bluish-green	7.2–8.2	42–55	*Scytonema* sp.
Bakreshwar, WB	Hot-spring	Bluish-green	8.2–9.1	44–57	*Scytonema* sp.

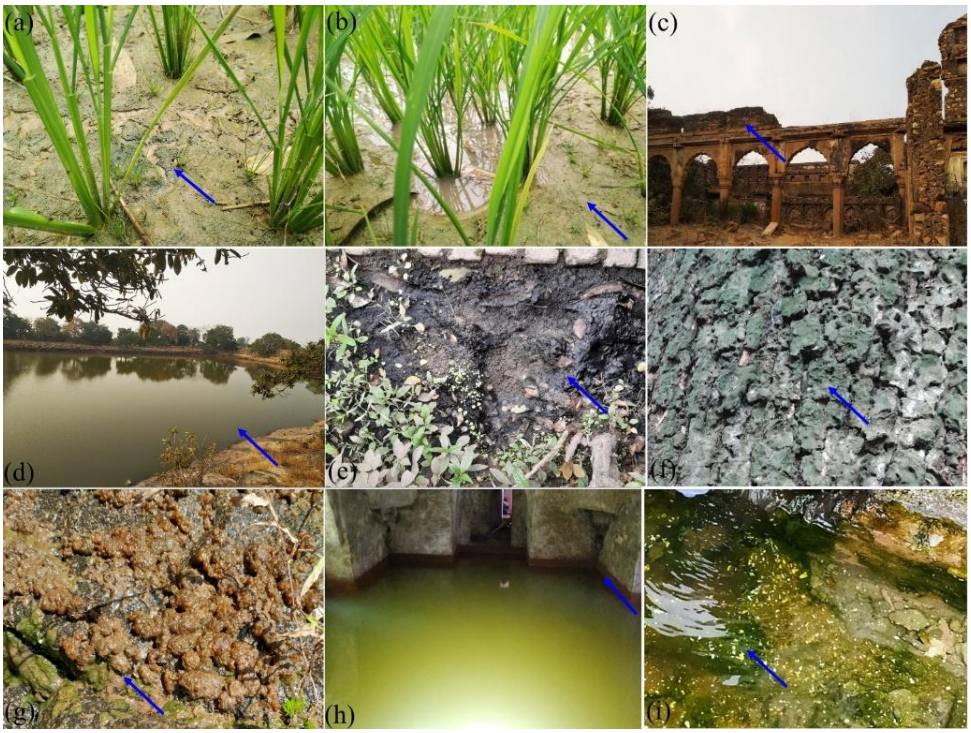

Figure 2. Diverse habitats of sampling sites. (a, b) Piparahwa, rice-field, (c, d) Vijaygarh Fort and Pond, (e) Soil mat, (f) Mango bark, (g) Rocky inhabitant near Dudh Dhara Waterfall, (h) Sohna Hot-Spring, and (i) Bakreshwar Hot-Spring. The arrow indicates cyanobacteria colonization in various habitats.

2.2. Microscopy and organism identification

The collected samples from diverse habitats were repeatedly washed with double-distilled water (DDW) to remove soil particles. A few colonies of each sample were crushed with mortar and pestle and infused in a liquid BG-11 medium with or without nitrogen supplements. Further, culture was spread and streaked on a Petri dish to grow under controlled white illumination (55.08 ± 9.18 µmol m^{-2} s^{-1}) at 24 ± 2 ℃ for 14/10 h in circadian oscillation. The newly obtained colony of cyanobacteria was purified and mass cultured for future purposes. From each sample, a 10 µL aliquot was taken onto a clean slide and examined under a bright-field microscope with 40X eyepiece (METZER-M 5000 TM EDGE, India) for the identification of cyanobacteria. Photographs were captured using Biowizard software with a digital camera associated with the microscope and analyzed using the same software.

2.3. Extraction, determination, and estimation of photopigments

The non-polar photosynthetic pigments (chlorophyll *a* and carotenoids) were extracted using the protocol summarized earlier by Lichtenthaler and Wellburn [12]. All the washed samples from diverse habitats were homogenized in methanol (90%) with overnight incubation at 4℃. Further, aliquots were centrifuged at 6000 rpm for 10 minutes, and supernatants were used for UV-Vis double-beam spectrophotometry (UV-1800 Shimadzu, Japan) analysis, ranging from 200 nm to 800

nm. Similarly, the hydrophilic phycobiliprotein pigment extraction was done as mentioned by Kannaujiya and Sinha [13]. Briefly, the cell pellets were harvested *via* centrifugation and washed twice using potassium phosphate buffer (50mM, pH 7.0). The cell pellets were sonicated with the same buffer along with 2.5% ethylenediaminetetraacetic acid (EDTA), 5% sucrose, and 1mM phenylmethylsulfonyl fluoride (PMSF). The suspension was then undergone for a freeze-thaw cycle (−20°C/4°C) until the change in the suspension color occurred. Finally, PBPs from cells were extracted by centrifugation at 12,000 rpm for 30 min at 4 °C. The supernatant was considered as crude PBPs and were likewise screened for their absorption maxima *via* spectrophotometry. To estimate the concentration of PC (phycocyanin), PE (phycoerythrin), and APC (allophycocyanin), equations described by Bennett and Bogorad were used [14].

2.4. Antioxidative enzyme assay

To assay the antioxidative enzymes of different cyanobacterial cultures, the protocol described earlier was followed [15]. Cyanobacterial cells were harvested and solubilized in 50 mM phosphate buffer containing 1mM EDTA, 1% (*w/v*) polyvinyl polyprollidone (PVP), and 2.5mM PMSF and sonicated for 10 min with 30s/20s pulse on/off (PRO650, Labman, India). The cell suspensions were then centrifuged at 12,000 rpm for 35 min. The derived supernatant served as an enzyme extract to assay enzymatic antioxidant activity. Assessment of catalase activity (CAT; EC 1.11.1.6) was done using the method of Aebi [16], where the decomposition rate of H_2O_2 was measured at 240 nm. Likewise, peroxidase activity (POD; EC 1.11.1.7) was quantified with the change of pyrogallol to purpurogallin at 420 nm [17] while superoxide dismutase (SOD; EC 1.15.1.1) activity was checked at 560 nm [18].

2.5. Extraction, partial purification, and spectrophotometric analysis of MAAs

Homogenized samples (30 mL) from diverse habitats were pelleted via centrifugation at 9000 rpm for 10 minutes. The resultant pellets were dissolved in 3 mL 100% HPLC-grade methanol (Qualigens®, Thermo Fisher Scientific India Pvt. Ltd.), followed by overnight incubation (4°C). Further, the cell suspension was centrifuged at 9000 rpm for 10 minutes, and the supernatants (methanolic extract) were collected in a fresh Eppendorf tube (2 mL) and proceeded for UV-Vis double beam spectrophotometry (UV-1800 Shimadzu, Japan). The spectra were imported onto the computer, and peaks were examined using UV-probe software. Methanolic extracts of the same were transferred onto a cleaned watch glass and subjected to evaporation through a vacuum evaporator (42°C). Further, residues were dissolved in Milli-Q water (2 mL). Purification of the same was accomplished by adding chloroform (100 µL) and subjected to vortex and centrifugation at 9000 rpm for five minutes. The resultant aqueous solutions were collected in a fresh Eppendorf tube and filtered through a nylon-based syringe filter (pore size 0.2 µm) (Axiva Sichem Biotech, New Delhi). This filtrate was considered partially purified MAAs and stored at 4°C before HPLC analysis.

2.6. Purification and HPLC analysis of MAAs

Analysis of partially purified MAAs were performed using a Semi Prep HPLC system (1525 Binary HPLC Pump, Waters, Pvt. Ltd.) equipped with a photodiode array (PDA) detector (Waters)

and SunFire®C18 OBD™ Prep Column (pore size: 100 Å, particle size: 5µm, inner diameter: 10 mm × length: 250 mm). The whole HPLC system was monitored using Empower-3 software (Waters). Acetic acid glacial (0.02% v/v) (extrapure AR, ACS, Exiplus™, 99.9%, SRL) was used as the mobile phase for the isocratic run with a flow rate of 3.0 ml min^{-1}. The partially purified MAAs samples (500 µL) were injected into the C18 column of the HPLC system using an autoinjector (Waters). The identification of UV-absorbing compounds (MAAs) was accomplished in the solvent by analyzing their specific absorption maxima and corresponding retention times.

2.7. Statistical analysis

The estimation of pigments and the antioxidative assay were performed in triplicate order. The corresponding results were measured as mean with standard deviation. To investigate the correlation in cyanobacterial metabolites, Pearson correlation matrix analysis was performed to interpret the functional relationship between pigment contents and enzymatic antioxidants with statistical significance at $P<0.05$.

3. Results

3.1. Microscopy and organism identification

From the selected geographical sites, cyanobacteria were identified on the basis of light microscopy and their morphological characteristics, correlating with the standard monographs and taxonomic keys by Desikachary [19] and Komárek [20] (Table 1). The two genera of cyanobacteria were recognized from rice-field of Sonbhadra, namely *Calothrix* sp., with long, straight trichomes, swollen at the base and tapering at the top. In addition, some trichomes had colorless sheathing, with the lower part of the filaments ending with short hairs (Figure 3a). Another cyanobacterium from the same habitat was identified as *Anabaena* sp., having green, gelatinous, straight trichomes with terminal, intercalary, and broader heterocysts (Figure 3b). Cyanobacteria collected from Vijaygarh Fort confirmed the presence of *Nostoc* sp. and *Aphanothece* sp. The cyanobacterium *Aphanothece* sp. (Figure 3d) was characterized with relatively small, hemispherical to barrel-shaped solitary cells lacking heterocysts, while another cyanobacterium, *Nostoc* sp., has mucilaginous filaments with prominent and clear heterocysts, intercalated in-between the vegetative cells (Figure 3c). The same cyanobacterium *Nostoc* sp. was also isolated from the near Dudh Dhara habitat with light blue-green filaments, hemispherical cells, and loosely elliptical arrangement (Figure 3g). We isolated the cyanobacterium *Oscillatoria* sp. with broad trichomes, longer cells, a straight apical portion, and no heterocysts from the campus of Banaras Hindu University, Varanasi (Figure 3e). Another cyanobacterium, *Lyngbya* sp., with long, unbranched filamentous cells, olive-green in color, with tortuous outer colorless sheaths, and non-heterocystous was also isolated from the same habitats (Figure 3f). From the Sohna hot-spring, Haryana, *Scytonema* sp. was isolated, with a dark green thallus, false branches, and more heterocysts at the intercalary position (Figure 3h). Contrarily, the same *Scytonema* sp. isolated from the Bakreshwar hot-spring, WB, exhibits pale blue-green filaments and barrel-shaped cells with false branching (Figure 3i).

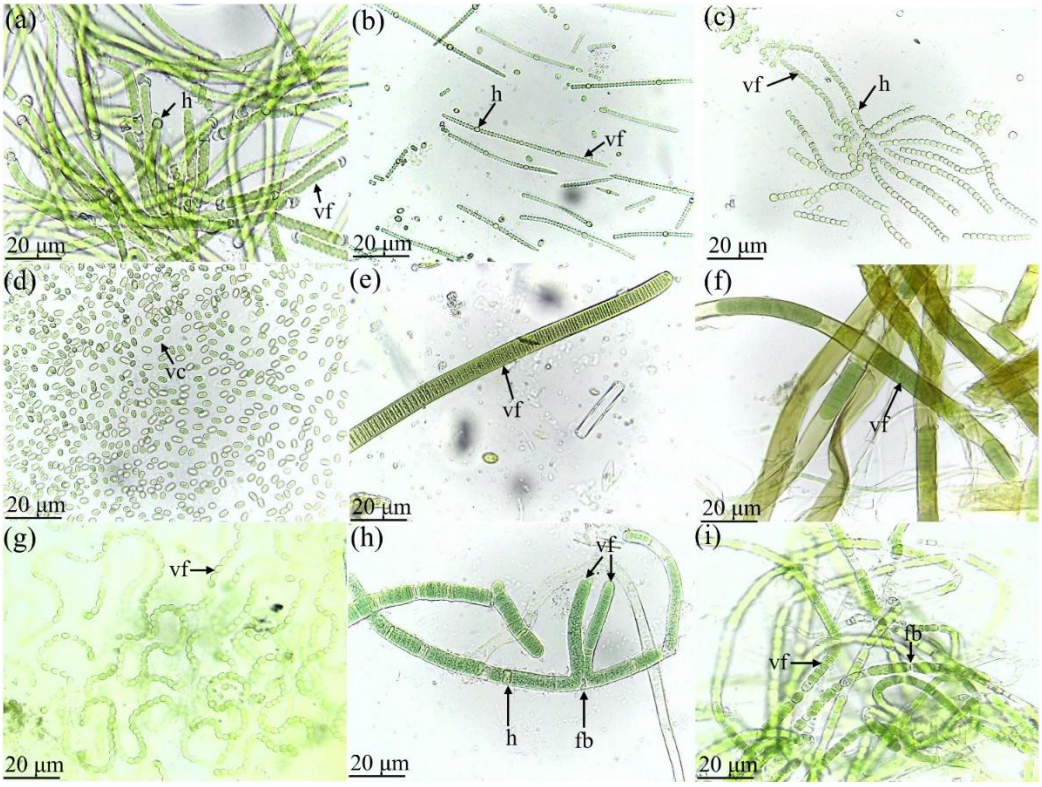

Figure 3. Cyanobacteria identified from diverse habitats of India. (a) *Calothrix* sp., (b) *Anabaena* sp., (c) *Nostoc* sp., (d) *Aphanothece* sp., (e) *Oscillatoria* sp., (f) *Lyngby*a sp., (g) *Nostoc* sp., and (h-i) *Scytonema* sp. h-heterocyst, fb-false branching, vc- vegetative cell, and vf-vegetative filament.

3.2. Analysis of photopigments

The isolated cyanobacteria showed a varied amount of photopigments due to their diverse habitats **(**Figure 4a**).** The rice-field (Piparahwa-P) cyanobacterium *Anabaena* sp. showed the maximum Chl *a* (7.635 ± 0.37 µg mL^{-1}), followed by *Nostoc* sp. from Vijaygarh Fort (VF) (6.485 ± 0.48 µg mL^{-1}). Total carotenoid content was found almost similar in both cyanobacteria *Anabaena* sp. (P) and *Nostoc* sp. (VF). The cyanobacterium *Lyngbya* sp. gave a contrary result with least Chl *a* (3.514 ± 0.02 µg mL^{-1}) content but third highest carotenoid content (2.514 ± 0.19 µg mL^{-1}) among the nine isolated cyanobacteria. The Chl *a* content of *Scytonema* sp. isolated from WB was measured half of the Chl *a* from the same isolate of Haryana hot-spring, while the carotenoid content was almost similar in both the species.

The spectrophotometric analysis of extracted phycobiliproteins (PBPs) revealed a variable content of subunits among the nine isolated cyanobacterial species. We found that all the three PBPs subunits, phycoerythrin (PE), phycocyanin (PC), and allophycocyanin (APC), were present in *Aphanothece* sp., *Lyngbya* sp., *Oscillatoria* sp., and *Nostoc* sp. from Dudh Dhara, while the rest of five isolates had only PC and APC (Figure 4b). The rice-field cyanobacterium *Anabaena* sp. recorded the highest PC concentration (0.17 ± 0.005 mg mL^{-1}) among all the isolates. A similar trend of PE, PC, and APC content were found in *Oscillatoria* sp. and *Lyngbya* sp., with the former having the maximum PE (0.089 ± 0.005 mg mL^{-1}). *Nostoc* sp. from Dudh Dhara showed an equal amount of

PE (0.081 ± 0.003 mg mL^{-1}) and PC (0.083 ± 0.008 mg mL^{-1}), while *Aphanothece* sp. recorded the highest APC content (0.054 ± 0.006 mg mL^{-1}) followed by hot-spring *Scytonema* sp. isolated from WB (Figure 4c).

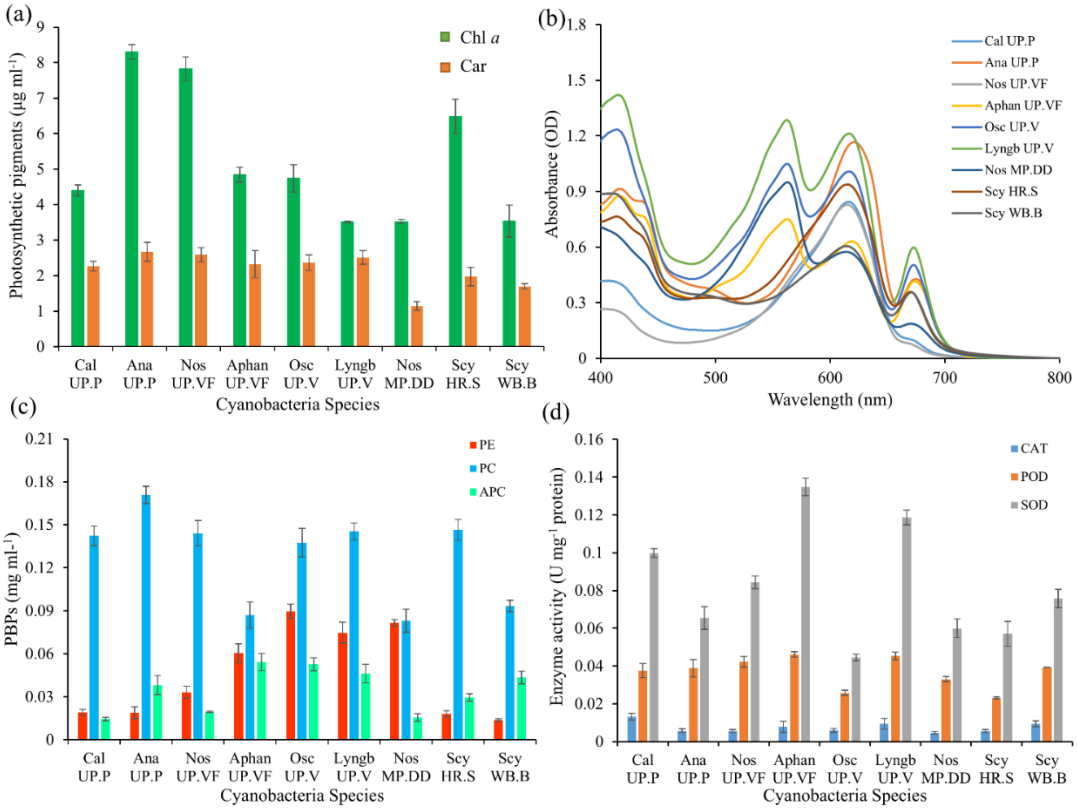

Figure 4. (a) Variation in the Chl *a* and carotenoid (Car) content; (b) absorption spectra of extracted PBPs; (c) estimation of PE, PC, and APC content from extracted PBPs; and (d) enzymatic antioxidative assay of SOD, POD, and CAT from nine cyanobacterial isolates namely: *Calothrix* sp. (Cal UP.P), *Anabaena* sp. (Ana UP.P), *Nostoc* sp. from Vijaygarh Fort (Nos UP.VF), *Aphanothece* sp. (Aphan UP.VF), *Oscillatoria* sp. (Osc UP.V), *Lyngbya* sp. (Lyngb UP.V), *Nostoc* sp. from Dudh Dhara (Nos MP.DD), *Scytonema* sp. from Haryana (Scy HR.S), and *Scytonema* sp. from West Bengal (Scy WB.B). Data are presented as mean (n = 3) and standard deviation as error bars. UP-Uttar Pradesh, P-Piparahwa, S- Sohna, V- Varanasi, VF- Vijaygarh Fort, DD- Dudh Dhara, MP-Madhya Pradesh, HR- Haryana, WB- West Bengal, and B-Bakreshwar.

3.3. Enzymatic antioxidant assay

The antioxidative enzymatic assay of cyanobacterial isolates was analyzed as a preliminary step towards the defense mechanism against superoxide radicals, which are produced in response to environmental stress. Among the three enzymes, the highest activity was observed by SOD followed by POD and CAT (Figure 4d). The cyanobacterium *Aphanothece* sp. showed the maximum SOD (0.134 ± 0.004 U mg^{-1} protein) and POD (0.46 ± 0.001 U mg^{-1} protein) activity, followed by *Lyngbya* sp. (SOD, 0.118 ± 0.003 U mg^{-1} protein; POD, 0.45 ± 0.002 U mg^{-1} protein). The least

activity was recorded in *Oscillatoria* sp., measured about 0.044 ± 0.001 and 0.025 ± 0.005 units of SOD and POD, respectively. However, *Calothrix* sp. resulted in the highest CAT activity (0.013 ± 0.001 U mg^{-1} protein), followed by *Lyngbya* sp. (0.009 ± 0.002 U mg^{-1} protein) and *Scytonema* sp. (0.009 ± 0.001 U mg^{-1} protein).

3.4. UV-Vis spectrophotometric analysis of partially purified MAAs

The absorption spectra of methanolic extracts showed different peaks for UV-absorbing compounds, MAAs (λ_{max} = 268–333 nm), chlorophyll *a* (λ_{max} = 430–435 nm and 665 nm), phycobiliproteins (λ_{max} = 618–620 nm), and carotenoids (λ_{max} = 450–475 nm). Further, the absorption spectrum of water-solubilized, partially purified MAAs recorded only a single broad peak between 275 and 350 nm, validating the presence of MAAs in the cyanobacterial samples.

3.5. Spectral screening and HPLC analysis of MAAs

The various peaks of MAAs from diverse habitat specific cyanobacteria were screened using HPLC chromatograms (Table 2). The HPLC chromatograms of major genera isolated cyanobacterium *Calothrix* sp. from the rice-field (Piparahwa) of the Sonbhadra district, exhibited peak at λ_{max} = 334 nm (RT = 11.2 min) (Figure 5a), while other cyanobacterium *Anabaena* sp., exhibited absorption maximum at 310 nm (RT = 11.1 min) (Figure 5b), which showed probability of MAAs, such as MAAs-334a and MAAs-310a, respectively. The second sampling site in the same geographical area was the Vijaygarh Fort. This site was predominantly characterized by the genera *Nostoc* sp. with MAAs-321 (λ_{max} = 321 nm and RT = 13 minutes) (Figure 5c) and *Aphanothece* sp. (λ_{max} = 275, 277, 290, and 296 nm, with RT = 3.2, 6.8, 16.1, and 17.5 minutes, respectively) (Figure 5d). Cyanobacteria sampled from the campus of Banaras Hindu University was primarily dominated by *Oscillatoria* sp., with absorption maxima (λ_{max}) at 331 nm and 320 nm, with retention times of 8.8 and 14.6 minutes, respectively (Figure 5e). The peaks absorption maxima analysed in this range indicates the probability of different types of MAAs, like MAAs-331 and MAAs-320a.

The other cyanobacterium from the same habitat, *Lyngbya* sp. showed three peaks at absorption maxima (λ_{max}) 313 nm, 320 nm, and 334 nm, with retention times of 2.8, 6.2, and 8.8 minutes (Figure 5f), indicating the possibility of certain MAAs, represented as MAAs-313, MAAs-320b, and MAAs-334b, respectively (Table 2). The Dudh Dhara waterfall, Amarkantak, Madhya Pradesh, was selected as the third location, mainly inhabited by *Nostoc* sp. The HPLC chromatogram from the genera, recorded at absorption maxima (λ_{max}) of 319, 320, and 322 nm with retention times (RT) of 5.2, 9.6, and 10.3 minutes, respectively (Figure 5g), signifies the presence of MAAs, such as MAAs-319, MAAs-320c, and MAAs-322, respectively. Geothermal springs of Sohna, Haryana, and Bakreshwar, WB, were the fourth site of collection, which prevailed with the presence of *Scytonema* sp. The extracted HPLC chromatogram showed absorption maxima (λ_{max}) at 310 and 320 nm, with retention times (RT) of 10.5 and 15.9 minutes, respectively (Figures 5h and i), which exhibit the presence of like MAAs-310b and MAAs-320d, respectively.

Table 2. Mycosporine-like amino acids from diverse habitats of cyanobacterial samples with their corresponding absorbance wavelength (λ_{max}), retention time (RT), and optical density (OD).

Habitats/sites	Cyanobacteria	RT (min)	λ_{max} (nm)	OD	Probable MAAs
Rice-field (Piparahwa)	*Calothrix* sp.	11.2	334	0.023	MAAs-334a
	Anabaena sp	11.1	310	0.015	MAAs-310a
Vijaygarh Fort (monument wall and pond)	*Nostoc* sp.	13.0	321	0.028	MAAs-321
	Aphanothece sp.	3.2	275	0.025	MAAs-275
		6.8	277	0.009	MAAs-277
		16.1	290	0.083	MAAs-290
		17.5	296	0.009	MAAs-296
BHU campus (soil mat and mango bark)	*Oscillatoria* sp.	8.8	331	0.012	MAAs-331
		14.6	320	0.006	MAAs-320a
	Lyngbya sp.	2.8	313	0.001	MAAs-313
		6.2	320	0.0021	MAAs-320b
		8.8	334	0.002	MAAs-334b
Dudh Dhara waterfall (Moist rocky surface)	*Nostoc* sp.	5.2	319	0.009	MAAs-319
		9.6	320	0.103	MAAs-320c
		10.3	322	0.003	MAAs-322
Sohna thermal spring	*Scytonema* sp.	10.5	310	0.089	MAAs-310b
Bakreshwar thermal spring	*Scytonema* sp.	15.9	320	0.005	MAAs-320d

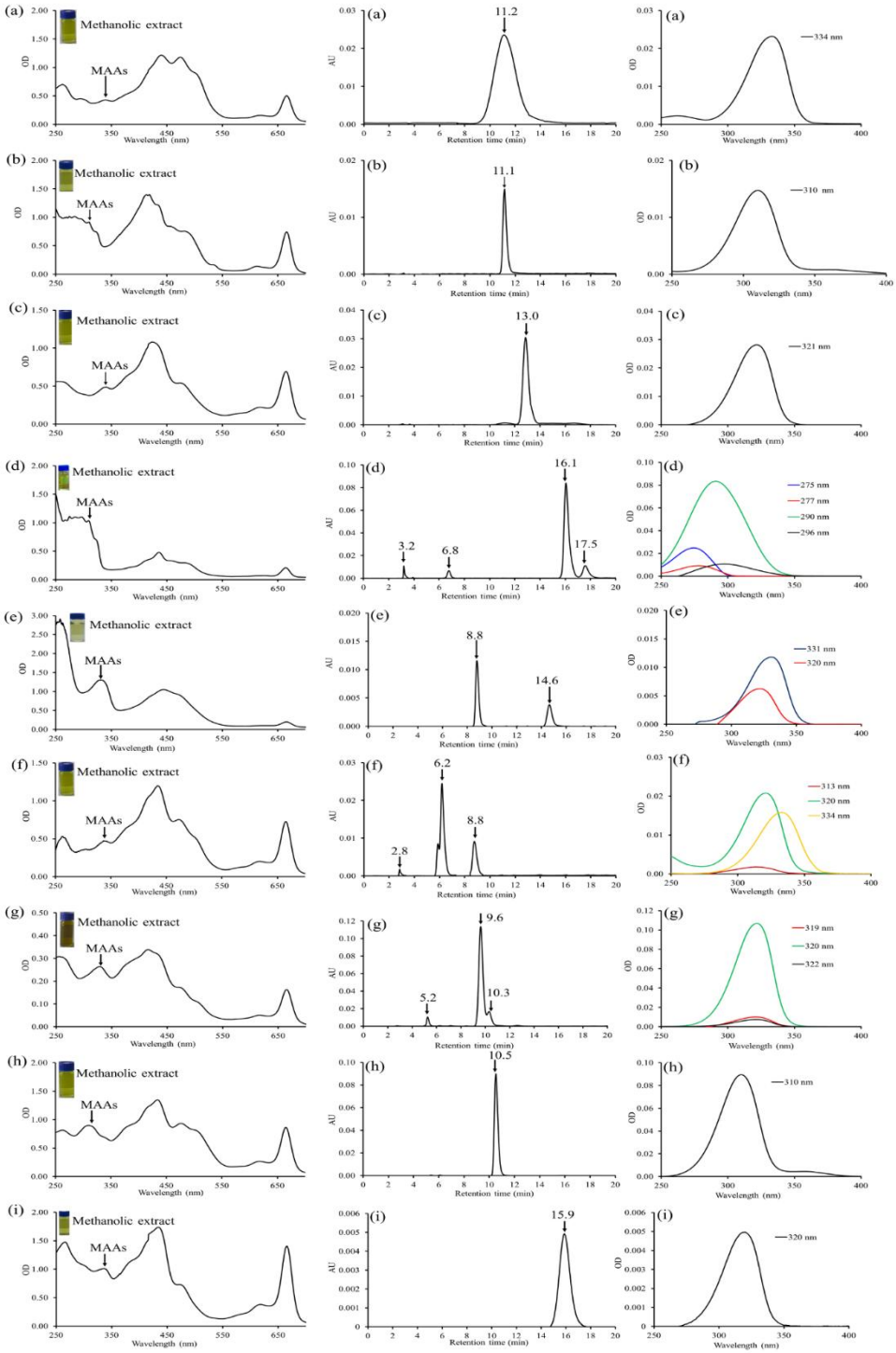

Figure 5. UV-Vis spectrophotometric absorption spectra of partially purified methanolic extract of diverse habitats cyanobacteria, HPLC chromatogram of purified MAAs with their absorbance maxima (λ_{max}) and corresponding retention times. (a, b) Rice-field-Piparahwa (*Calothrix* sp., *Anabaena* sp.), (c, d) Vijaygarh Fort (*Nostoc* sp., *Aphanothece* sp.), (e, f) BHU campus (*Oscillatoria* sp., *Lyngbya* sp.), (g) Dudh Dhara waterfall (*Nostoc* sp.), (h) Sohna thermal spring (*Scytonema* sp.), and (i) Bakreshwar thermal spring (*Scytonema* sp.). 'OD' stands for optical density and 'AU' for arbitrary unit; readings were taken via spectrophotometer and HPLC, respectively.

3.6. Correlation analysis

The correlation between photopigments (Chl *a*, carotenoids, PBPs) and antioxidative enzymes (CAT, POD, SOD) was evaluated *via* Pearson Correlation matrix. Chlorophyll content showed positive correlation only with carotenoid (0.585) and PC (0.694), while carotenoids exhibit the maximum correlation with PC, APC, and all the antioxidative enzymes (Table 3). Among the three PBPs subunits, a positive correlation was only with PE and APC. The antioxidative enzymes showed a strong correlation with each other (0.576, 0.643, 0.843) and APC.

Table 3. Pearson Correlation Matrix analysis among photopigments and antioxidative enzymes. The values indicate positive and negative correlation with each other, while * symbolizes significant $P<0.05$.

	Chl *a*	Car	PE	PC	APC	CAT	POD	SOD
Chl *a*	1	0.585	−0.552	0.694*	−0.282	−0.518	−0.062	−0.210
Car	0.585	1	−0.120	0.725*	0.420	0.152	0.344	0.316
PE	−0.552	−0.120	1	−0.274	0.193	−0.067	−0.028	0.111
PC	0.694*	0.725*	−0.274	1	−0.006	−0.207	−0.168	−0.252
APC	−0.282	0.420	0.193	−0.006	1	0.631	0.195	0.383
CAT	−0.518	0.152	−0.067	−0.207	0.631	1	0.576	0.643
POD	−0.062	0.344	−0.028	−0.168	0.195	0.576	1	0.843*
SOD	−0.210	0.316	0.111	−0.252	0.383	0.643	0.843*	1

4. Discussion

In the evolutionary history of photosynthetic microorganisms, cyanobacteria are the oldest organisms that have persisted with the evolving Earth. They have a great ability to survive under harsh environmental conditions such as high temperature, high solar radiation, and high moisture, which enables them to exist in various ecological conditions [21].

In this study, we visited four geographical sites to collect cyanobacteria samples. The Sonbhadra, UP, was selected for the collection of rice-field, ponds, and monuments inhabiting cyanobacteria. Rice-field ecosystems prevailing in the tropics are often exposed to high solar radiation and temperature. This type of vegetation serves as a nutrient-rich environment and habitat for varied cyanobacterial species [22]. Similarly, cyanobacteria *Nostoc* sp. and *Anabaena* sp. have been reported in many such rice-field surveys, while the association of *Anabaena* with *Azolla* has been widely studied for their agroeconomical benefits [23].

In our study, *Calothrix* sp. and *Anabaena* sp. mostly dominated in the collected sample from the rice-field [24]. Keshari and Adhikary reported diverse cyanobacterial species collected (Nostacales and Stigonematales orders) from different Indian monuments with blackish-brown characteristics [25]. Similarly, blackish brown samples on the surface of the Vijaygarh Fort wall were identified as *Nostoc* sp., while *Aphanothece* sp. isolated from the pond correlated with the presence of phytoplankton. Two genera, *Oscillatoria* sp. and *Lyngbya* sp., were identified on the soil surface and bark of mango trees, respectively, at the BHU campus, Varanasi, UP. The cyanobacterium *Oscillatoria* sp. was entangled to form a black mat-like appearance on the soil surface. This correlated with the study of *Oscillatoria*, aging of soil biocrust reported by Zhang et al. [26]. *Lyngbya* sp., inhabiting the bark of

the mango tree, showed similar morphological identification as described [27]. The sample collected from Dudh Dhara waterfall, Amarkantak, MP, was identified as *Nostoc* sp. Its appearance on the moist rocky surface was brownish and bluish-green. The following habitats selected for cyanobacteria sampling were Sohana geothermal spring, Haryana, and Bakreshwar geothermal spring, WB. In these two geographical sites, the dominant genera collection was identified as *Scytonema* sp. It inhabited a blue-green mat-like appearance in both hot-springs. Except for *Nostoc* sp. and *Scytonema* sp., which were reported in two sites, none of the identified genera were common. A similar study reported the presence of *Nostoc* sp. strain HKAR-2, *Scytonema* sp. strain HKAR-3 from hot-spring, Rajgir, India [28].

The nine isolated samples from different habitats exhibited varied photosynthetic pigment compositions and antioxidative enzymatic activities, which were influenced by pH, temperature, light intensity, and nutrient resources depending on their native source [29]. The rice-field environments are subject to high solar radiation, including PAR, UVR, and high temperatures in the tropics, and salts (fertilizers, pesticides, or insecticides) [30]. An excess of physicochemical parameters proves to be a stress to the inhabiting cyanobacteria. Thus, cyanobacteria of rice-field habitat have shown higher defense strategies against abiotic stresses [31]. The reported rice-field isolates, *Calothrix* sp. and *Anabaena* sp., have also shown high enzymatic antioxidant activity and photopigments in response to the environmental factors. Similarly, *Aphanothece* sp. showed the highest defense properties in terms of antioxidative enzymes and carotenoids. The *Lyngbya sp*. from mango bark showed the presence of all PBPs (PE, PC, and APC) in higher amount along with carotenoids, SOD, POD, and CAT. Cyanobacteria growing on tree bark are continuously exposed to UV radiation, desiccation, and relative humidity, with variations in light intensity and temperature, which induce the synthesis of many photoprotective compounds [32]. This correlates with the physiological parameters found in our study as an insight into survival strategies by *Lyngbya* sp. against environmental fluctuation. Similar to trees, monuments also face the same abiotic stresses and develop mitigation strategies [25]. The cyanobacterium *Nostoc* sp. from Vijaygarh Fort has shown high enzymatic antioxidative activity and photosynthetic pigments as an adaptation towards the habitat. All the selected sites had pH levels as slightly neutral to alkaline, with moderate temperature (except for the hot-spring), which favors cyanobacterial growth. Low temperatures (< 30°C) and alkaline pH (> 7) are favorable conditions for the luxuriant growth of cyanobacteria. However, thermophilic cyanobacteria enable morphological modifications to survive and flourish in extremely hot environments. For instance, *Scytonema* sp. reported in hot-springs may produce sheaths, while others secrete exopolysaccharides (EPSs) from their cells to guard against drying out [33]. Various molecular adaptations, including thermostable enzymes and photoprotective compounds, improve metabolism, photosynthesis, and stress signal transmission [28,34].

Being phototrophic in nature, cyanobacteria are solely dependent on light energy for their survival. However, UV rays along with solar radiation, are detrimental toward their survivability. Usually, UV-B radiation causes detrimental effects on proteins, lipids, DNA, and other macromolecules, which influences photosynthesis efficiency, development, and premature cell death. To counterbalance these negative effects, cyanobacteria have developed many defense systems, including UV-absorbing compounds such as scytonemin and mycosporine-like amino acids (MAAs) [10,35–37].

Apart from cyanobacteria, several additional species, including macroalgae, phytoplankton, lichens, fungi, coral, and fish, have been recorded to collect MAAs [4,38]. Besides being small, hydrophilic secondary bioactive compounds, MAAs have additional features, including antioxidant,

anti-aging, wound-healing, and stress-reducing actions, which enhance their commercial value in the pharmaceutical and cosmeceutical sectors [3]. Screening of MAAs *via* HPLC from various habitats of cyanobacteria showed a slight variation in the retention time at the same absorption maxima (λ_{max} = 310, 320, 334 nm), indicating the presence of different types of novel MAAs. Each MAA has specific structural orientation that influences their chromatographic behavior [39]. The HPLC absorption wavelength (λ_{max}) of MAAs-310a-b, 331, 334a-b, 320a-d, 321, 322 nm revealed five novel kinds of MAAs in diverse cyanobacteria. The selected wavelengths were characterized as, 310 nm = mycosporine-glycine, 331 nm = mycosporine-2-glycine, 334 nm = porphyra-334, and shinorine and 320-322 nm = palythine. The absorption wavelength (λ_{max}) at 310 nm was screened in two cyanobacteria, *Anabaena* sp. (MAAs-310a) and *Scytonema* sp. (MAAs-310b), collected from a rice-field and the Sohna thermal spring, respectively. The same wavelength (λ_{max} = 310 nm) compound has been reported as mycosporine-glycine in the rice-field cyanobacterium *Anabaena doliolum*, which helps protection against UV-A and UV-B radiation [40]. However, a peak at λ_{max} = 331 nm (MAAs-331) was found in a single genus, *Oscillatoria* sp., isolated from the BHU campus (soil mat). The absorption wavelength of MAAs-331 exhibits probable resemblance with reference MAAs, such as mycosporine-2-glycine, which was also found in many cyanobacteria, such as *Euhalothece* sp. [41], *Arthrospira* [42], and *Aphanothece halophytica* [43]. Furthermore, MAAs having absorbance maxima with 334 nm detected at RT of 11.2 and 8.8 minutes in two different sheathing genera, such as *Calothrix* sp. (MAAs-334a), and *Lyngbya* sp. (MAAs-334b). The MAAs-334a and MAAs-334b were found in the absorption range (λ_{max} = 334 nm), which indicates the presence of probable MAAs such as porphyra-334 (11.2 min) and shinorine (8.8 min) [44.45]. Porphyra-334 and shinorine have been also documented in various cyanobacteria, such as *Aphanizomenon* [46], *Nostoc commune* [47], and *Nodularia* [48]. Interestingly, UV-radiation absorbing capacity of both porphyra-334 and shinorine extracted from *Porphyra umbilicalis* exhibits considerable promise as a natural UV protective sunscreen and marketed under the name Helioguard®365 [49,50].

The spectral peak (λ_{max}) at 320-322 nm is the most common screened MAA found in most habitats, except for rice-fields cyanobacteria. The *Nostoc* sp. isolated from Vijaygarh Fort (VF) has shown a single peak of MAAs-321 nm, whereas *Nostoc* sp. isolated from near Dudh Dhara waterfall has shown two HPLC peaks of MAAs-320c and MAAs-322. Earlier findings of these wavelength ranges (λ_{max} = 320–322), suggested as palythine and its derivatives, have been confirmed in other genera of cyanobacteria, including *Nostoc commune* [47], *Nostoc* sp. UHCC 0302 [51], *Pseudanabaena* sp. CCNU1 [52], *Lyngbya* [53], and *Leptolyngbya* sp. [54]. The MAAs indicated that numerous cyanobacterial species isolated from a wide range of Brazilian ecological zones are abundant sources of various palythine formulations [55].

Database and published articles on MAAs analysis indicate that all the tentatively identified MAAs having absorption maxima 310–334 nm possess UV-protective, antioxidant, anti-inflammatory, and anti-aging properties [50,56,57]. The cyanobacterium *Lyngbya* sp., which inhabited bark of the mango tree, also exhibits diverse spectral profile (λ_{max} = 320 and 334 nm) of MAAs, which may safeguard against a broad range of UV radiation. Similarly, palythine derived from *Lyngbya* sp. HKAR-15 possesses potent antioxidant properties and offers quick and efficient photoprotection [53]. Based on the absorbance value of MAAs, cyanobacterial strains such as *Nostoc* sp., *Scytonema* sp., and *Lyngbya* sp. are most promising for commercial-scale MAA production. Correlating the photopigments and antioxidants profile of the nine cyanobacteria, carotenoids

exhibited the highest correlation with all other factors except PE. This was due to the fact that carotenoids function both as pigment as well as a potent antioxidant [58]. However, chlorophyll content exhibited a linear relation with pigments like PC and carotenoids, which indicate most important accessory photopigments for cyanobacterial growth and photosynthesis. PE and APC positive correlation with enzymatic antioxidants signifies for their importance as strong antioxidants apart from photopigments [59,60].

5. Conclusions

This study was performed to determine the presence of antioxidants, pigments, and UV-absorbing photoprotective chemicals, broadly mycosporine-like amino acids (MAAs), from diverse habitats of cyanobacteria. From the nine isolates of cyanobacteria, *Nostoc* sp. and *Scytonema* sp. were found in two different niches, while the other five, including *Calothrix* sp., *Anabaena* sp., *Aphanothece* sp., *Oscillatoria* sp., and *Lyngbya* sp., were present as single genera. Based on their native environmental condition, the cyanobacteria showed varied amounts of photopigments (Chl *a*, carotenoids, PBPs), antioxidant enzymes (SOD, POD, CAT), and UV-absorbing compounds. Further, HPLC analyses of partially purified MAAs revealed that presence of different MAAs with prominent absorption peaks at specific wavelengths (λ_{max} = 310, 320, 321, 322, 331, and 334 nm). The absorbance maxima of these peaks were similar with previously characterized MAAs, such as mycosporine glycine, palythine, mycosporine-2-glycine, shinorine, and porphyra-334. Moreover, six other distinct peaks at specific wavelengths (λ_{max} = 275, 277, 290, 296, 313, and 319 nm) were observed, which indicate the possibility of entirely novel and uncharacterized MAAs compounds. This study also suggests that isolated cyanobacteria could be helpful for the mass production of pigments, antioxidative enzymes, and novel sunscreen compounds for biotechnological applications.

Author contributions

Ram Lal: Conceptualization, data collection, data curation, formal analysis, methodology, writing-original draft. Megha Jaiswal: data collection, data curation, formal analysis, helped in the experiment, and writing-original draft. Nasreen Amin: helped in sampling. Vinod K. Kannaujiya: provided laboratory facilities and generated the idea, designed all the experiments, critically reviewed, and edited the whole manuscript.

Use of Generative-AI tools declaration

The authors declare they have not used Artificial Intelligence (AI) tools in the creation of this article.

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Conflict of interest

The authors declare that they have no conflict of interest.

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