

MULTIFUNCTIONAL ASPECT OF MYCOSPORINE LIKE AMINO ACIDS: A REVIEW

Prathima R¹, Harsha TS², and Nagalambika Prasad^{1*}

^{1*}Department of Microbiology, School of Life Sciences, JSS Academy of Higher Education and Research (Deemed to be University), Mysuru, Karnataka, Pin code: 570015, India.

²Department of Environmental Science, Karnataka State Open University, Mukthagangotri, Mysuru-570 006, India.

ABSTRACT

Organisms have evolved mechanisms to preserve selves from harmful ultraviolet radiation embracing from the earth's crust. One of such classes is the UV engrossing compounds such as mycosporine-like amino acids. Mycosporine-like amino acids (MAAs) are a faction of small secondary metabolites, found in the cytoplasm of organisms that are bare to high light intensity. They are usually colorless, uncharged, water solvent ampholytes that display sub-atomic weight ranging from 188 to 1050 Da. They are well known for Photoprotection. However, their role is not limited only to photoprotection but there is evidence for additional functioning of these molecules. This review is on the multifunction of MAAs as antioxidant, inflammation, photoaging, oxidative stress, desiccation stress, thermal stress, nitrogen storage, and other functions.

Key words: Mycosporine-like amino acids (MAAs), Multifunction

INTRODUCTION

Mycosporine-like amino acids are colorless, uncharged, water-solvent ampholytes that display sub-atomic weight going from 188 to 1050 Da. They are very small secondary metabolites synthesized by the organisms that are exposed to high-intensity sunlight, normally marine conditions. MAAs are bright (UV) retaining small molecules, giving screening assurance across highly active photons in the UV-A frequency [1]. Solid stability is because MAAs acquire amazingly large molar termination coefficients (ϵ) ($\epsilon = 28,100-50,000 \text{ mol}^{-1} \text{ cm}^{-1}$) [2]. The historical backdrop of examination on MAAs traces back to the last part of the 60s of the only remaining century, since the revelation of MAAs information remembering data for their structure, properties, functions, and distribution is continually creating.

These UV-engrossing pigments were first recognized during 1960 and the essential manufactured plan of an MAA, for the present circumstance an infectious metabolite related by light-actuated sporulation, was reported a few years later [3,4]. It immediately ended up being clear that these UV engrossing mixtures are incredibly far and wide in nature. They are found in numerous cyanobacteria and conceivably in a few different

Corresponding Author:
ambikap1604[at]gmaildotcom

Receiving Date: May 11, 2020
Acceptance Date: June 25, 2020
Publication Date: June 27, 2020

prokaryotes also [5], in eukaryotic microorganisms (yeasts, algae, and microorganisms), just as an assortment of marine macroalgae, corals, and other marine living things, as well as vertebrate and invertebrates creatures, get these mixtures from their feed [6].

MAAs remain in the cytoplasmic content and external sheath of cyanobacteria and other algae like Dinoflagellates, and serve as filters to forbid UV damage prevention [7-9]. All MAA particles contain a central cyclohexenone, in other words, cyclohexenimine chromophore of an amino acid or its imino alcohol nitrogen substituent, including absorption maximum of 268 to 362nm. Based on the variety of nitrogen substitutes and connected side groups the structure and absorption of MAAs may change [10]. The economic and biotechnological exploitation of these secondary metabolites is varied. This allows MAAs to be used as cell proliferation activators in cosmetics and toiletries as well as UV protection products [11-13]. Some MAAs were found to preserve fibroblast cells from cell death caused by UV exposure [14] and UV-induced maturing in individual skin [15]. The MAAs have antioxidant activity and shape to protect the skin defence system and the expression of Hsp70. MAAs like tetrahydropyridine products were used as sunscreen specialists monetarily. In addition, MAAs are fitted with two monetary products (Helioguard® and Helionori®) from the red algae. *Porphyra umbilicalis* is in retail presently [16]. Shockingly, MAA synthesis is greater in photoheterotrophic development than in photoautotrophic development, CO₂ and light can go about as restricting components [10]. Their biological production is probably obtained via our knowledge of the genetic basis of their synthesis and yet limited enzyme activity from a mixture of amino acids through the shikimate pathway.

More than 30 different mycosporine compound designs have been explained so far [17]. Various glycosylated mycosporine subordinates are included. Mycosporine-glutaminol-glucoside, and mycosporine-glutamicol-glucoside have been recently described in aquatic yeasts, microcolonial ascomycetes and terrestrial fungi [18-20]. The amount and form of MAA contained in cells vary depending on the species, topographical area, and environment (for example, nitrate concentration). There are also methods for constructing the MAA material, such as illumination with various UVR or light sources and nitrate compound treatment. MAAs also been used as photostabilizing added substances in paints, varnishes, and plastics in addition to UV protectants [17]. Other than photoprotection, this study focuses on few multifunctional aspects of MAA are as follows.

Multifunctional Role of MAAs:

1. Antioxidant properties of MAAs:

Some MAAs are able not just to protect the cell from absorbing and scattering UV light (high energy Photons), but also from scavenging of reactive oxygen species such as singlet oxygen, hydroxyl radicals and hydroperoxyl radicals. The high-temperature sensitivity of scleractinic coral *Stylophorapistillata* (33°C) causes damage to the photo-synthetic equipments and a huge rise in the movement of the catalase and superoxide dismutase. However, a comparable study in *Platygyrorykyensis* has no influence on the enzyme levels. The crucial thing in *Platygyra* of MAA-glycine was a 20-overlay. However no other MAA were detected until the compounds were completely depleted in *Stylophora* and severely reduced in *Platygyra* as oxidative stress happens, and the amount of intracellular mycosporine-glycine reduces dramatically.

The impact of O₂, provided by the enlightenment of methylene blue or eosine Y, on electron transport in mitochondria, hemolysis of erythrocytes, lipid peroxidation, and growth of *Escherichia coli* has been investigated in greater depth to see whether mycosporine-glycine can protect organic frameworks from photodynamic harm by quenching singlet oxygen. Taking everything into account, mycosporine-glycine expansion stifled singlet oxygen-initiated damage. It had been suggested that some MAAs could, in any event, contribute to shielding organic marine organisms against sole-light damage, by filtering harmful UV radiation and by scavenging ¹O₂ from endogenous photo-sensitizers [21].

During the day, photosynthetic activity by the zooxanthellae (symbiotic) in corals will cause neighbourhood oxygen supersaturation up to 373 percent air immersion [22]. In gypsum covering on the lower part of saltern dissipation lakes in Israel, Eilat, inhabited by a thick local area of MAA-rich unicellular cyanobacteria, oxygen concentrations as high as 350μM were measured, equivalent to around 450 percent oxygen immersion at the temperature and encompassing saltiness, as depicted in more noteworthy profundity in the accompanying segment [23].

2. Salt stress and MAAs:

The higher the cell's intracellular solute fixations must be, the higher the cell's salt focus. Most microorganisms accumulate low subatomic weight, mostly uncharged natural particles, which fill in as alleged "viable solutes" or "osmotic solutes" to provide the fundamental osmotic equilibrium. The MAAs that accumulate in the cytoplasm of the cell is also tiny uncharged natural particles that contribute to the cell's osmotic pressing factor. In this way, the issue of how much MAAs can be applied to the conversion of microorganisms to high salt concentrations (saline) can be raised. MAAs are only rarely present in large amounts in cyanobacteria that sprout in freshwater environment. The recent discovery of MAAs in a *Microcystis* freshwater blossom [24] appears to be an unusual special case. In either case, cyanobacteria regularly produce high centralizations of MAAs in hypersaline and saline environments. The most remarkable case described is the massive growth of cyanobacteria ('*Euhalothece*' type) within bottom of the ocean, gypsum covering Israel's Eilat saltern vanishing lake. The crust is only protected by a few centimetres of brine, with the intention of exposing the cells to light forces nearly as intense as full sunlight. The intracellular centralization of MAAs in these cells is estimated to be 100mM or 3% of the cells' wet weight, according to the findings [25]. However, it is most likely the highest MAA concentrations ever discovered, with values as high as 0.8 percent of dry weight of the cell in *Gleocapsa* [26].

Furthermore, measurements of MAAs in the cell can give close to 5% of the absolute intracellular osmo-electrolyte fixation needed for osmotic equilibrium, with trehalose and glucose known as the fundamentally viable solutes. UV light was required during MAA biosynthesis in a test arrangement where cells were energy-incubated with sucrose in the dark. Although a collection of shinorine was normally confined to levels of UV-B radiation, the synthesis of mycosporine-glycine was saltiness-controlled and synergistically upgraded by UV-B. Hypoosmotic stun caused spillage of MAA (especially mycosporine-glycine) to the medium due to the Eilat gypsum crust [27]. When fluctuation of temperature in the outside causes enormous shifts in sea ice brine salinity, MAAs can be linked to the transition of sea ice algae to osmotic changes [28].

The halophilic black yeasts like *Cladosporium cladosporioides*, *Cladosporium sphaerospermum*,

Hortaea werneckii and *Phaeothea triangularis*, and the halotolerant *Aureobasidium pullulans* (all in the order *Dothideales*) all have mycosporine-glutamicol-glucoside as their main mycosporine. Dark yeast, on the other hand, has lower levels of mycosporine-glutaminol-glucoside. At 10% salt, these fungi grow and produced significantly more mycosporine-glutaminol-glucoside than when grown in the medium without salt. In some extremophilic dark yeasts exposed to saline production medium, this substance may thus act as a beneficial viable solute. In high-salt-grown cells, the proportions of mycosporine-glutamicol-glucoside were reduced to some extent. Not all dark yeasts behave in this way: *Trimmatostromasalinum* did not develop entirely specific mycosporine levels when the salt concentration was increased [29].

3. Desiccation stress and MAAs:

There have been several reports of high mycosporine concentrations in microorganisms which are exposed to drought stress, such as cyanobacteria [30,31] and colonial fungi that live in rocks [32]. The cyanobacterium *Nostoc commune* has a thick extracellular lattice where glycosylated MAAs are implanted in its characteristic living room, which is subjected to synchronous pressures of parching, oxidation, and UV radiation.

In its investigation of blue green algae on the outsides of the natural soil in India, Tirkey and Adhikary (2005) [30] expressed that MAA is reinvigorated by the drying-up and illumination blend, which uncovers organic organisms, through filamentous sheath shapes including *Plectonema*, *Scytonema* and *Lyngbya*. However, this inference was not supported by evidence from the trial. *Gloeocapsa sp.*, a unicellular cyanobacterium, was used in the experiments. The existence of this compound may be linked to the parasites' vegetative hyphae's endurance capacity and life span [32].

4. Thermal stress and MAAs:

There are a few records on MAA arrangement enlistment by high-temperature tension. During concurrent UV-opening thematic pressure (increased water temperature to 32°C) upgraded the amount of MAA in the delicate corals, *Sinularia flexibilis* and *Lobophytum compactum* in the Great Barrier Reef [33,34]. However, unlike UV and salt pressure, increasing temperature stress, as well as cold stun, supplement restriction, and photooxidative pressure did not initiate MAA arrangement in the cyanobacterium *Chlorogloeopsis* PCC 6912 [27]. Due to the high incidence of microorganisms producing MAA in chilly marine habitats, multipurpose MAAs will most likely act under viable solo circumstances of freezing; a detailed investigation of the mycosporine cold resistance has still to be done in any case.

5. MAAs as sunscreen ingredients:

In many organic entities and locations around the world a link between mycosporine content and in situ irradiation levels has been observed. Two example of situations in which strong light exposure led to MAA collection are the *Phaeocystis pouchetii* dinoflagellate and *Guinardia striata* diatom (=

Rhizosoleniastolterfothii) [35], UV light induced shinorine acceptance in the cyanobacteria *Anabaena sp.*, *Scytonema sp.*, and *Nostoc commune* [36], as well as the acceptance of porphyra-334 and shinorine in Antarctic diatoms [37]. In the presence of photosynthesis-active radiation and UV radiation the photoprotective potential of mycosporine-glutaminol-glucoside [18] was dramatically increased [38]. The two *Rhodotorulasshowed* large concentrations of mycosporine-glutaminol-glucoside following the enlistment of UV radiation (up to 0.5 per cent of dry weight), suggesting that this secondary metabolite should be combined to shield the stress from UV.

UV-B rays having short wavelength also induces an adjustment in the general measures of the various MAAs formed in *G. dorsum*, with shorter wavelengths being absorbed more readily [39]. In the Antarctic centric diatoms *Thalassiosira sp.*, visible light is best for enlisting MAA synthesis. Furthermore, *Corethroncriophilum* [37], and in such situations, the MAA enlistment activity range peaks in the 370–460 nm frequency range [40]. Garcia-Pichel and colleagues calculated the possibility of MAAs acting as sun-screen microalgae compounds. MAAs are suitable compounds because they maintain frequencies that enter deeply into the water. Frequencies below 300 nm are more dangerous to DNA and other cell segments, but they do not penetrate as deeply into the water and therefore pose a lesser threat to the cell. In most cases, MAA does not account for more than 1% of a cell's dry weight [6,26]. The Euhalothece found in hypersaline environments, as described below [25], may be an eminent special case. Only cells larger than 100 µm can infer almost no assurance from MAAs disintegrated in the cytoplasm, so the accumulated sunscreens will be effective only in those cells [26,41,42]. When the efficacy of MAAs in single planktonic cells or trichomes is called into question, their accumulation in planktonic sprouts can help to increase UV protection in the surrounding region [43]. The viability of MAAs could potentially be improved by bundling the shades around radiation-sensitive locations inside the cell [44,34]. The ghastly absorbance of flawless cells in the UV range was generally tiny, corresponding to the enormous amounts of absolute MAA released after freezing and defrosting of the cells, according to research on the dinoflagellates *Heterocapsa triquetra* and *Alexandriumtamarense*. The finding could be explained by the MAAs' nonhomogeneous transport inside the cell [45]. Limited MAA selection in *Nostoc*'s extracellular sheath can provide productive protection [46].

6. MAAs as accessory pigments:

MAAs were suggested to improve photosynthetic effectiveness in an early study [47]. MAAs were discovered to be fluorescent mixtures at that time. Upon UV-A excitement, fluorescence outflow was found in frequencies approaching the absorption of Chlorophyll a sordid band, which implied the transfer of energy from MAA to chlorophyll. MAAs, however, are, if any, weakly fluorescent, with most MAAs in high-light settings, in which light energy is not confined to photosynthesis.

7. MAAs as a source of intracellular nitrogen:

MAAs are mixtures of nitrogen containing compounds, with the most abundant forms having two nitrogen particles per atom. MAAs have also been suggested to function as an intracellular nitrogen stockpiling system [48]. The MAA (porphyra-334 and shinorine) arrangement was observed in the red macroalgae *Porphyra columbina* on the Patagonian coast to be induced by ammonium particles and UV

light. Algal circles were brooded in the presence of 0,50 and 300 M NH₄⁺ in this study; the greatest emphasis was much more MAA than the smaller fixations. If MAAs are to be used as intracellular nitrogen storage, nitrogen preparedness equipment should be available if other acceptable nitrogen types are difficult to produce.

8. Fungal reproduction and mycosporines:

In fungi, light, especially UV light, is frequently needed for the arrangement of conceptive organs. Light-activated shades that ingest at 240 and 310 nm are used to detect it. Colonies produced in the dark do not sporulate because they lack UV-absorbing pigments. The ingestion maxima of most of these mixtures are at 310 nm, and they are referred to as 'P310'. After it was isolated from the basidiomycete *Stereumhirsutum sporophores*, the principal P-310 material was known as mycosporiniserinol [49,3]. The abbreviation 'P310' refers to three compounds that assimilate differently at frequencies other than the most extreme 310 nm, and they also differ in their sporogenic activity. Following that, a few more mycosporines were isolated from different fungi. Mycosporines are now known to occur in all fungal groups, including *Ascomycetes*, *Deuteromycetes*, *Basidiomycetes*, and *Zygomycetes*. However, certain phylogenetic ancestries, such as the *Wallemiales* [50], *Agaricales* [4], *Sporidiobolales*, and *Cystofilobasidiales*, are lacking them [38]. Only oxo-carbonyl mycosporines were contained in earthly lichens with fungal cyanobacterial symbioses [51], which were possibly delivered by the fungal accomplice. Mycosporine-delivering fungi may be terrestrial or aquatic, phytopathogenic or saprophytic, and some can be opportunistic pathogens. They can be found in fresh or salty environments as filamentous on a various substratum.

The mycelia of a few terrestrial fungal genus, close to UV rays-incited sporogenic mycosporines (P-310 metabolites) were identified, but they were not present in the nonsporulating colonies which are filled with obscurity. The parasite *Pyronema omphalods* are found in the Ascomycete category. Primordial cultures with various mycosporine compounds and Nor-mycosporine-glutamine were detected during the growth of fruiting bodies. The concentration decreased when the lifestyle is ageing, whereas the development of ascoma, notably ascospores, showed an increased mycosporine-glutaminol glucoside [52]. The biogenetic substance change of nor-mycosporine presumably happens during ascospore arrangement, passing on simultaneously a reformist synthetic steadiness of the last compound. Another mycosporine is delivered during proliferation and aggregated in spores in the phytopathogenic anamorphic *Ascochyta fabae* [17]. After those underlying disclosures, mycosporins or their biochemical history are related with sporulating mycelia and employed as biochemical markers for fungi in regenerative settings or as propagatory markers [32].

The sporulated hymenium of UV-activated mycelium and sclerotia, but not non-differential mycelia, rhizomorphs or non-sporulated mycelia has been consistently observed in the ascomycetes or comparable combinations. As a result, the mycosporine mixture and occurrence seemed to be closely linked to the sporulation interaction [49,17,51]. The conidiogenous thallus had the most notable fixations (both full scale and miniature conidia), the perithecial thallus had the intermediate fixations, and the vegetative mycelium had the least [52,17]. The number of mycosporines produced during thallus formation and their filling within spores describes movement from combination region to conceptive cells [17,32].

CONCLUSION

The UV engrossing compounds mycosporine-like amino acids (MAAs) produced as a small secondary metabolites, that are colorless, uncharged, and usually small in size, found in the cytoplasm of the organisms that are exposed to high-intensity containing sunlight. They commonly function as photoprotection. Shreds of evidence show mycosporine-like amino acids have a multifunctional role other than photoprotection. Little-known applications of mycosporine-like amino acids are mentioned in the review as MAAs functioning as an antioxidant, salt stress, desiccation stress, thermal stress, as a sunscreen agent, MAAs as accessory pigments, as a source of intracellular nitrogen, and other functions.

REFERENCES

1. Schmid D, Schürch C, Züllli F, Nissen HP, Prieur H. Mycosporine-like amino acids: Natural UV-screening compounds from red algae to protect the skin against photoaging. *SÖFW-journal*. 2003;129(7):38-42.
2. Wada N, Sakamoto T, Matsugo S. Multiple roles of photosynthetic and sunscreen pigments in cyanobacteria focusing on the oxidative stress. *Metabolites*. 2013 Jun;3(2):463-83.
3. Favre-Bonvin J, Arpin N, Brevard C. Structure de la mycosporine (P 310). *Canadian Journal of Chemistry*. 1976 Apr 1;54(7):1105-13.
4. Arpin N. Mycosporines: mise au point et données nouvelles concernant leurs structures, leur distribution, leur localisation et leur biogenèse.
5. Arai T, Nishijima M, Adachi K, Sano H. Isolation and structure of a UV absorbing substance from the marine bacterium *Micrococcus* sp. AK-334. *Marine Biotechnology Institute, Tokyo, Japan*, pp. 88-94. 1992.
6. Karentz D, McEuen FS, Land MC, Dunlap WC. Survey of mycosporine-like amino acid compounds in Antarctic marine organisms: potential protection from ultraviolet exposure. *Marine Biology*. 1991 Feb;108(1):157-66.
7. Llewellyn CA, Airs RL. Distribution and abundance of MAAs in 33 species of microalgae across 13 classes. *Marine drugs*. 2010 Apr;8(4):1273-91.
8. Carreto JI, Carignan MO. Mycosporine-like amino acids: relevant secondary metabolites. *Chemical and ecological aspects*. *Marine drugs*. 2011 Mar;9(3):387-446.
9. Wada N, Sakamoto T, Matsugo S. Mycosporine-like amino acids and their derivatives as natural antioxidants. *Antioxidants*. 2015 Sep;4(3):603-46.
10. Singh SP. Study on mycosporine-like amino acids (MAAs) in cyanobacteria: A biochemical, bioinformatics and molecular biology approach.
11. Conde FR, Churio MS, Previtali CM. The photoprotector mechanism of mycosporine-like amino acids. Excited-state properties and photostability of porphyra-334 in aqueous solution. *Journal of Photochemistry and Photobiology B: Biology*. 2000 Jul 1;56(2-3):139-44.
12. Torres A, Enk CD, Hochberg M, Srebnik M. Porphyra-334, a potential natural source for UVA protective sunscreens. *Photochemical & Photobiological Sciences*. 2006;5(4):432-5.
13. Whitehead K, Hedges JI. Photodegradation and photosensitization of mycosporine-like amino acids. *Journal of Photochemistry and Photobiology B: Biology*. 2005 Aug 1;80(2):115-21.
14. Oyamada C, Kaneniwa M, Ebitani K, Murata M, Ishihara K. Mycosporine-like amino acids extracted from scallop (*Patinopecten yessoensis*) ovaries: UV protection and growth stimulation activities on human cells. *Marine Biotechnology*. 2008 Mar;10(2):141-50.
15. Schmid D, Schürch C, Züllli F. Cosmetic skin care products and cosmetic agents for protecting skin against premature aging. Patent No. EP1473028. 2004 Nov;3.

16. Katoch M, Mazmouz R, Chau R, Pearson LA, Pickford R, Neilan BA. Heterologous production of cyanobacterial mycosporine-like amino acids mycosporine-ornithine and mycosporine-lysine in *Escherichia coli*. *Applied and environmental microbiology*. 2016 Oct 15;82(20):6167-73.
17. Bandaranayake W. Mycosporines: are they nature's sunscreens?. *Natural product reports*. 1998;15(2):159-72.
18. Volkmann M, Whitehead K, Rütters H, Rullkötter J, Gorbushina AA. Mycosporine-glutamicol-glucoside: a natural UV-absorbing secondary metabolite of rock-inhabiting microcolonial fungi. *Rapid Communications in Mass Spectrometry*. 2003 May 15;17(9):897-902.
19. Libkind D, Diéguez MC, Moliné M, Pérez P, Zagarese HE, van Broock M. Occurrence of photoprotective compounds in yeasts from freshwater ecosystems of northwestern Patagonia (Argentina). *Photochemistry and photobiology*. 2006 Jul;82(4):972-80.
20. Volkmann M, Gorbushina AA. A broadly applicable method for extraction and characterization of mycosporines and mycosporine-like amino acids of terrestrial, marine and freshwater origin. *FEMS Microbiology Letters*. 2006 Feb 1;255(2):286-95.
21. Suh HJ, Lee HW, Jung J. Mycosporine Glycine Protects Biological Systems Against Photodynamic Damage by Quenching Singlet Oxygen with a High Efficiency. *Photochemistry and photobiology*. 2003 Aug;78(2):109-13.
22. Shashar N, Cohen Y, Loya Y. Extreme diel fluctuations of oxygen in diffusive boundary layers surrounding stony corals. *The Biological Bulletin*. 1993 Dec 1;185(3):455-61.
23. Canfield DE, Sørensen KB, Oren A. Biogeochemistry of a gypsum-encrusted microbial ecosystem. *Geobiology*. 2004 Jul;2(3):133-50.
24. Liu Z, Häder DP, Sommaruga R. Occurrence of mycosporine-like amino acids (MAAs) in the bloom-forming cyanobacterium *Microcystis aeruginosa*. *Journal of Plankton Research*. 2004 Aug 1;26(8):963-6.
25. Oren A. Mycosporine-like amino acids as osmotic solutes in a community of halophilic cyanobacteria. *Geomicrobiology Journal*. 1997 Jul 1;14(3):231-40.
26. Garcia-Pichel F, Castenholz RW. Occurrence of UV-absorbing, mycosporine-like compounds among cyanobacterial isolates and an estimate of their screening capacity. *Applied and Environmental Microbiology*. 1993 Jan;59(1):163-9.
27. Portwich A, Garcia-Pichel F. A novel prokaryotic UVB photoreceptor in the cyanobacterium *Chlorogloeopsis* PCC 6912. *Photochemistry and Photobiology*. 2000 Apr;71(4):493-8.
28. Arrigo KR, Thomas DN. Large scale importance of sea ice biology in the Southern Ocean. *Antarctic Science*. 2004 Dec 1;16(4):471.
29. Kogej T, Gostinčar C, Volkmann M, Gorbushina AA, Gunde-Cimerman N. Mycosporines in extremophilic fungi—novel complementary osmolytes?. *Environmental Chemistry*. 2006 May 26;3(2):105-10.
30. Tirkey J, Adhikary SP. Cyanobacteria in biological soil crusts of India. *Current Science*. 2005 Aug 10;515-21.
31. Wright DJ, Smith SC, Joardar V, Scherer S, Jervis J, Warren A, Helm RF, Potts M. UV irradiation and desiccation modulate the three-dimensional extracellular matrix of *Nostoc commune* (Cyanobacteria). *Journal of Biological Chemistry*. 2005 Dec 2;280(48):40271-81.
32. Gorbushina A. Microcolonial fungi: survival potential of terrestrial vegetative structures. *Astrobiology*. 2003 Nov 1;3(3):543-54.
33. Michalek-Wagner K. Seasonal and sex-specific variations in levels of photo-protecting mycosporine-like amino acids (MAAs) in soft corals. *Marine Biology*. 2001 Oct;139(4):651-60.
34. Shick JM, Dunlap WC. Mycosporine-like amino acids and related gadusols: biosynthesis, accumulation, and UV-protective functions in aquatic organisms. *Annual review of Physiology*. 2002 Mar;64(1):223-62.
35. Llewellyn CA, Harbour DS. A temporal study of mycosporine-like amino acids in surface water phytoplankton from the English Channel and correlation with solar irradiation. *Marine Biological Association of the United Kingdom. Journal of the Marine Biological Association of the United Kingdom*. 2003 Feb 1;83(1):1.
36. Sinha RP, Klisch M, Helbling EW, Häder DP. Induction of mycosporine-like amino acids (MAAs) in cyanobacteria by solar ultraviolet-B radiation. *Journal of Photochemistry and Photobiology B: Biology*. 2001 Jul 1;60(2-3):129-35.

37. Helbling EW, Chalker BE, Dunlap WC, Holm-Hansen O, Villafañe VE. Photoacclimation of Antarctic marine diatoms to solar ultraviolet radiation. *Journal of Experimental Marine Biology and Ecology*. 1996 Oct 25;204(1-2):85-101.
38. Libkind D, Pérez P, Sommaruga R, del Carmen Diéguez M, Ferraro M, Brizzio S, Zagarese H, van Broock M. Constitutive and UV-inducible synthesis of photoprotective compounds (carotenoids and mycosporines) by freshwater yeasts. *Photochemical & Photobiological Sciences*. 2004;3(3):281-6.
39. Sinha RP, Klisch M, Gröniger A, Häder DP. Mycosporine-like amino acids in the marine red alga *Gracilaria cornea*—effects of UV and heat. *Environmental and Experimental Botany*. 2000 Feb 1;43(1):33-43.
40. Riegger L, Robinson D. Photoinduction of UV-absorbing compounds in Antarctic diatoms and *Phaeocystis antarctica*. *Marine Ecology Progress Series*. 1997 Dec 15;160:13-25.
41. Roy S. Strategies for the minimisation of UV-induced damage. The effects of UV radiation in the marine environment. 2000 Mar 9:177-205.
42. Garcia-Pichel F. The absorption of ultraviolet radiation by microalgae: simple optics and photobiological implications. *Scientia Marina*. 1996 Dec 1;60(SUPPL. 1):73-9.
43. Sinha RP, Klisch M, Gröniger A, Häder DP. Ultraviolet-absorbing/screening substances in cyanobacteria, phytoplankton and macroalgae. *Journal of Photochemistry and Photobiology B: Biology*. 1998 Dec 1;47(2-3):83-94.
44. Neale PJ, Banaszak AT, Jarriel CR. Ultraviolet sunscreens in *Gymnodinium sanguineum* (Dinophyceae): mycosporine-like amino acids protect against inhibition of photosynthesis. *Journal of Phycology*. 1998 Dec;34(6):928-38.
45. Laurion I, Blouin F, Roy S. Packaging of mycosporine-like amino acids in dinoflagellates. *Marine Ecology Progress Series*. 2004 Sep 28;279:297-303.
46. Böhm GA, Pfliederer W, Böger P, Scherer S. Structure of a novel oligosaccharide-mycosporine-amino acid ultraviolet A/B sunscreen pigment from the terrestrial cyanobacterium *Nostoc commune*. *Journal of Biological Chemistry*. 1995 Apr 14;270(15):8536-9.