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Research Article

Response of the Cyanobacterium *Fischerella* Sp. Strain HKAR-5 against Combined Stress of UV-B Radiation, PAR and Pyrogallic Acid

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- Antioxidative enzymes
- Photosynthetic activity of PSII

Abstract

Combined effects of ultraviolet-B (UV-B; 280-315 nm) radiation, photosynthetically active radiation (PAR; 400-700 nm) and different concentrations (0, 5, 25 and 50 mg/L) of pyrogallic acid (PA) were studied on the key physiological and biochemical processes in the cyanobacterium *Fischerella* sp. strain HKAR-5. Responses of the cyanobacterium in terms of oxidative stress, pigmentation, total protein contents and photosynthetic activity of PSII (F_v/F_m) were assessed. Antioxidative enzymes showed dose-dependent increase in activities with increasing concentrations of PA along with UV-B and PAR till 48 h of exposure followed by a decrease on further exposure. Similar trend was observed for total carotene and proteincontents. Increasing duration of UV-B exposure along with variable concentrations of PA under PAR, resulted in the increase in total carotene and proteincontentstill 36h of exposure, followed by gradual decrease with increasing time duration. Concentration of Chl *a* declined up to 9 fold after 72 h of exposure and maximum decrease in photosynthetic activity of PSII was observed after 60 h of treatment of UV-B, PA (50 mg/L) and PAR. Present findings suggest that manifold enhancement in antioxidative enzymes with depressed photosynthetic rate are the active defence mechanisms adopted by the cyanobacterium *Fischerella* sp. strain HKAR-5 for its survival against combined stress of UV-B, PAR and variable doses of PA.

ABBREVIATIONS

UVR: Ultraviolet Radiation; PAR: Photosynthetically Active Radiation; F_v/F_m: Photosynthetic activity of PSII; PA: Pyrogallic Acid.

INTRODUCTION

Cyanobacteria, the prokaryotic photoautotrophic assemblage, are amongst the most successful and oldest life forms on this Earth. These ecologically and evolutionary important organisms are found in almost every plausible habitat on Earth [1]. They act as natural biofertilizers with the ability to fix atmospheric nitrogen into the assimilatory form (NH_4^+) [2], thus contributing to the nutrient cycling.

Highly energetic UV-B radiation, coming along with solar radiation, can damage cells by directly affecting DNA and proteins and indirectly via the reactive oxygen species (ROS) [3]. Ultraviolet radiation (UVR) actively influences morphology, cell differentiation, survival, growth, pigmentation, motility and orientation, phycobiliprotein composition, N_2 metabolism, protein profile, DNA and $^{14}CO_2$ uptake in cyanobacteria [4-7] and is major stress factor for phytoplankton [8]. Though only small fractions of UV-B (<1 % of the total solar radiation) reaches on the Earth's surface, it is potentially very active as can absorbed by important biomolecules such as nucleic acids, lipids and proteins and ultimately have fatal effects on biological systems. Cyanobacteria are exposed to lethal doses of UV-B (280-315 nm) and UV-A (315-400 nm) radiation in their natural brightly lit habitats while harvesting solar energy for photosynthesis and nitrogen fixation processes [9]. In long evolutionary history, cyanobacteria have undergone several modifications to maintain versatile physiology and wide ecological tolerance by evolving many mitigation strategies such as avoidance, scavenging of ROS by enzymatic and non-enzymatic antioxidant molecules as well as UV-absorbing/screening compounds viz., scytonemin and mycosporine-like amino acids (MAAs), UV-induced DNA damage repair and resynthesis of proteins and programmed cell death to counteract the deleterious effects of UVR [10-15].

Pyrogallic acid (PA) is widely distributed in nature and is commonly used in many industrial and consumer products [16]. Despite its beneficial properties, PA-mediated toxicity has been a major concern for almost all vital organs exposed to it. It was

reported that PA showed mutagenic effect and liver, lung, kidney and gastrointestinal tract were its major target organs [17]. Recently, PA as strong allelochemical attracted great attention. Release of the allelochemicals by the submerged macrophytes was considered to be an approach to inhibit the growth of phytoplankton [18,19]. PA also influence the metabolism of cyanobacteria and play important role in ROS production, disintegration of cell membrane integrity and DNA strands breaks (DSB) [10].

In the present study we have made an attempt to investigate the combined effects of PA, UV-B and PAR on the cyanobacterium *Fischerella* sp. strain HKAR-5 in terms of its antioxidative enzymatic activities, pigmentation, protein content and its photosynthetic efficiency.

MATERIALS AND METHODS

Growth conditionsand experimental organisms

The experimental organism, *Fischerella* sp. strain HKAR-5 was isolated from rocks of Mount Abu, Rajasthan, India and morphological identified by using standard taxonomic keys and monographs [20] and molecularly by *16S rRNA* gene amplification. *Fischerella* sp.strain HKAR-5 is the member of Nostocales and family Hapalosiphonaceae. The thallus is branched filamentous and heterocystous. The cyanobacterial culture were routinely grown in a culture room under axenic conditions in an autoclaved BG-11 (without nitrogen sources) medium [21] at a temperature of 28 ± 2°C and under continuous fluorescent white light of 12 Wm^{-2}. The cyanobacterial strain has been acclimatized in laboratory conditions since last seven years at a temperature of 28 ± 2°C.The cultures were hand shaken 4 times daily to avoid shelf shading and clumping. All experiments were performed with exponentially growing cultures.

Experimental setup

In the present study, PA was used as the model allelochemical compound and *Fischerella* sp. strain HKAR-5 as the test species. The homogeneous cyanobacterial samples (250 mL of culture in each petri dish with $OD_{750\ nm}$ = 0.73 ± 0.2 for a path length of 1 cm) were exposed to artificial UV-B radiation in a UV-chamber in four sterile open glass petri dishes (120 mm in diameter) with different concentrations (0, 5, 25 and 50 mg/L) of PA (Spectrochem, Mumbai, India). PA showed the strongest inhibitory activity to *Microcystisaeruginosa* with 50% effective concentration (EC_{50}) of 0.65-2.97 mg/L [22-23]. In natural aquatic environments, allelochemicals are continuously released into the surrounding water at low concentrations [22]. The concentrations of PA used in this study were higher than the concentrations secreted by aquatic macrophytes in natural water bodies.The UV-chamber was setup by fitting white cool fluorescent Osram L 36 W/32 Lumilux de luxe warm white and Radium NL 36 W/26 universal white; Germany for visible light and UV-B TL 40 W/12 fluorescence tubes (Sankyo Denki, Japan) for source of UV-B radiation. The distance of the UV-B tube in the chamber from the sample was adjusted to have a UV-B intensity of ~0.5 W m^{-2}. To avoid any exposure of UV-C radiation, each Petri dish was covered with 295 nm cut-off filter foils (Ultraphan; Digefra, Munich, Germany). During course of treatment (up to 72 h), all experimental cultures were exposed with constant temperature of 25 ± 2^0C. The heating and self-shading effects of cells were avoided by shaken culture at regular intervals. 35 mL of irradiated samples were withdrawn after each regular interval (12 h) of exposure and were then harvested by centrifugation and subjected to further study. Besides, one Petri dish without allelochemical and UV-B radiation was exposed under continuous PAR that served as control.50 mg/L dose of PA was selected as maximum dose as dose higher than this was lethal to the organism.

Determination of antioxidant enzyme activity

In order to assay the changes occurring in concentration of antioxidant enzymes during course of experiment, cell extracts were prepared after sonication in extraction buffer containing 50 mM phosphate buffer (pH 7.5), 2.5 mM phenylmethanesulfonyl fluoride (PMSF), 1 mM ethylene diamine tetra acetic acid (EDTA) and 1% (w/v) polyvinylpyrrolidone (PVP) with addition of 5 mM ascorbate and 20% sorbitol (w/v) for ascorbate peroxidase (APX) (EC 1.11.1.11) assay. The extraction buffer suspension was sonicated by using ultrasonicat or (Sonic and Materials, USA) and centrifuged at 10,000×g for 25 min at 4°C. The supernatant was separated carefully in another test tube and used for the analysis of enzymes. Catalase (CAT) activity (EC 1.11.1.6) was determined, by method developed by Rao et al. [24]. Reaction mixtures contained 2.86 mL phosphate buffer (pH 7.5), 4.4 mM H_2O_2 and 100 µL of enzyme extract. CAT activity was determined spectrophotometrically at 240 nm by recording O_2 release from enzymatic dissociation of H_2O_2 in darkness for 5 min. APXactivity was determined by measuring the decrease in absorbance of ascorbate oxidation to mono-dehydroascorbate at 290 nm [25]. Reaction mixture consisted of 2 mM ascorbate, 0.1 mM H_2O_2 (120 µL) and 800 µL of enzyme extract. Superoxide dismutase assay (SOD) (EC 1.15.1.1), measures the inhibition in the photochemical reduction of nitroblue tetrazolium (NBT). In spectrophotometric assay the reaction product was measured at 560 nm as method described earlier by Donahue et al. [26]. The reaction mixture of 2.1 mL contained 1.5 mL, 0.1 mM EDTA, 13 mM Met, 75 µm nitrobluetetrazolium and 2 µm riboflavin in 50 mM phosphate buffer (pH 7.8)and 600 µL of cell extract. Riboflavin was added at last and the reaction was initiated by placing the tubes under two 15-W fluorescent lamps. The reaction was terminated after 10 min by remova1 from the light source. Peroxidase (POD) activity (EC number 1.11.1.x) was measured by taking the absorbance at 420 nm, reaction mixtures included 0.1 M phosphate buffer pH 6.0, 5.33% pyrogallol solution (M/V), 3% H_2O_2 as substrate and 100 µL of enzyme extract as earlier method described by Britton and Mehley [27].

Determination of protein

Sample (5 mL) was taken test tube (in triplicate), 2 mL of reagent C was added, followed by incubation at room temperature for 10 min. Then reagent D was added to the test tubes and incubated for 30 min. O.D. was taken at 660 nm against BG-11 media as a blank using UV-VIS spectrophotometer. Total soluble protein was calculated by the method as described by Lowry et al. [28]. Proteins were quantified by using bovine serum albumin as standard.

Estimation of pigments

Cyanobacterial samples (5 mL) of *Fischerella* sp.strain HKAR-5 was centrifuged at 10,000 g for 10 min and pellet was dissolved

in desire volume of methanol (100%) in a test tube. It was kept for 24 h at 4°C and re-centrifuged at 10,000 g for 5 min. Spectra were taken at 200-700 nm against methanol as a blank by using UV-visible spectrophotometer (Hitachi 2900, Japan). The cellular Chl *a* and total carotene contents were calculated by using equations described by Dere et al. [29].

Determination of photosynthetic activity of PSII (F_v/F_m)

The treated cyanobacterial samples of *Fischerella* sp.strain HKAR-5 were dark-adapted for 30 min to allow complete oxidation of PSII reaction centres and the minimum (F_0) and maximum (F_m) fluorescent yields of PSII in the dark-adapted state were determined. The yields of both F_0 and F_m were used to calculate the photosynthetic activity of PSII (F_v/F_m) by the formula described by Schreiber [30]. The value of F_v/F_m was determined by using PAM fluorometer (PAM-2500, Heinz Walz GmbH, 2008, Effeltrich, Germany).

Statistical analysis

The experiments were repeated thrice for accuracy of the results. All results are presented as mean values of three replicates and statistical analyses were done by one way analysis of variance (ANOVA).Once a significant difference was detected post-hoc multiple comparisons were made by using the Tukey test (SPSS 16.0). The level of significance was set at 0.05 for all tests.

RESULTS AND DISCUSSION

Combined effects of UV-B, PAR and PA on enzymatic antioxidants

We observed about 3 fold (0.9910 µmol.min^{-1}mg^{-1} protein) gradual enhancement in APX activity under given stress condition (combined effects of UV-B radiation, PAR and different doses of pyrogallic acid) and maximum induction was observed in 48h duration of exposure of 50 mg/L of PA. However, APX activity declined to 1.5 fold (0.22 µmol.min^{-1}mg^{-1}protein) till 72h of exposure as compared to control. Comparatively more activity of APX was induced in samples with 25 mg/Land 50 mg/LPA (Figure 1A). In POD assay, sample with 50 mg/Lof PA showed maximum induction of POD (0.523U POD mg^{-1} proteins) at 48h of exposure which was 2.5 folds higher than control. POD activity decreased sharply (2 fold) on 72 h of exposure (Figure 1B). CAT activity gradually increased in all treated sample till 48h of exposure and it was maximum in 50 mg/L of PA containing sample (0.714 U CAT mg^{-1} proteins, 2 fold enhancements from control). After 48h of exposure, the CAT activity sharply declined. It decreased 1 fold at 72h exposure (0.2311 U CAT mg^{-1} proteins) in comparison to control (Figure 1C). In SOD assay, no enhancement in SOD activity was observed till 24h of exposure, however, in 36h of exposure, 25 mg/L and 50 mg/L of PA containing sample showed significant enhanced activity of SOD. The maximum activity of SOD enzyme were observed in 50 mg/L PA sample and it was enhanced about 3 fold (0.987 U SOD mg^{-1} proteins). After that, the activity decreased and at 72 h, the activity decreased to 2.5 fold in comparison to control (0.132 U SOD mg^{-1} proteins) (Figure 1D).

Effect on proteins

We observed that the total protein content exceeded up to 2 fold (0.0217 mg/mL) of total initial concentration (control) at 36h of exposure in 50 mg/LPA containing culture. However, after 36 h, it started decreasing and declined gradually up to 72h of exposure (1 fold, 0.0097 mg/mL) (Figure 2A).

Effects on photosynthetic efficiency of PSII (F_v/F_m)

There were strong correlations between values of F_v/F_m and healthiness of cyanobacterial sample. For instance, the control sample has 0.413 F_v/F_m value at 0 h exposure and it was much more than the other treated samples. The F_v/F_m value for the sample with 50 mg/L PA concentration exposed with PAR and UV-B, decreased up to 48 h exposur**e** and the value decreased to about7 fold (F_v/F_m value at 48 h exposure is 0.0551). The value for 60 and 72 h exposure was more or less same. The value of the F_v/F_m gradually declined in treated samples and it was sequentially less in 50, 25 and 5mg/LPA containing sample (Figure 2B).

Effects on photosynthetic pigments

Prolonged exposure of UV-B, PAR and PA causes leaching of Chl *a* from cyanobacterial cells and finally leads to breakage of filaments. Chl *a* content of cyanobacterial cells varied with exposure time and decreased continuously with duration of exposure. Maximum Chl *a* was found in non-treated sample (10.160 µg/gfw)**,** however it reduced to 9 fold after 72 h of exposure of the stress (Figure 3A). Total carotene contents of cyanobacterial cells increased initially till 36h of exposure to 1.5fold (2.36µg/gfw), followed by a decrease with increasing duration of exposure of samples and it reduced to 1.5fold (0.863µg/gfw) on 72h of exposure **(**Figure 3B).

In the present study, first time, combined effects of variable concentration of PA under constant exposure of UV-B radiation with PAR was studied. Attempts have been made to study the response of different defence mechanisms adapted by cyanobacterium *Fischerella* sp. strain HKAR-5 under exposed stress. We investigated the intracellular O_2^-, H_2O_2 and OH^- generation induced by PA, PAR and UV-B radiation in *Fischerella* sp. strain HKAR-5 in terms of antioxidative enzymes activities. We found that PA significantly induces the dose-dependent generation of O_2^- and consequently H_2O_2 and OH^- under constant UV-B stress with PAR. The exposure of UV-B and PA under PAR has synergistic effects on ROS generation. Low concentration of PA (5 mg/L) has comparatively low influence on inductive synthesis of antioxidative enzymes as compared to higher concentrations of PA (25 mg/L and 50mg/L), but was inhibited gradually with time of exposure (h). In our studies, 48 h exposure of stress was the optimum duration for maximum synthesis of antioxidative enzymes i.e. APX, POD, CAT and SOD. Similarly, total proteins and carotene contents increased to 2 folds and 1.5 folds respectively in sample with 50 mg/L PA. However there was continuous decrease in Chl *a* contents (9 folds) which may be due to bleaching/or photoreduction of photosynthetic pigments, disintegration of thylakoid lamellae. The value of photosynthetic activity of PSII (F_v/F_m) showed that PA and UV-B are strong photosynthetic inhibitors and the effective inhibitory concentration of PA was 50 mg/L at 24 h of exposure. The value of F_v/F_m was higher in control which seems to be in healthier condition and with increase of PA concentration; it decreased and became more or less constant after 60 h of exposure.

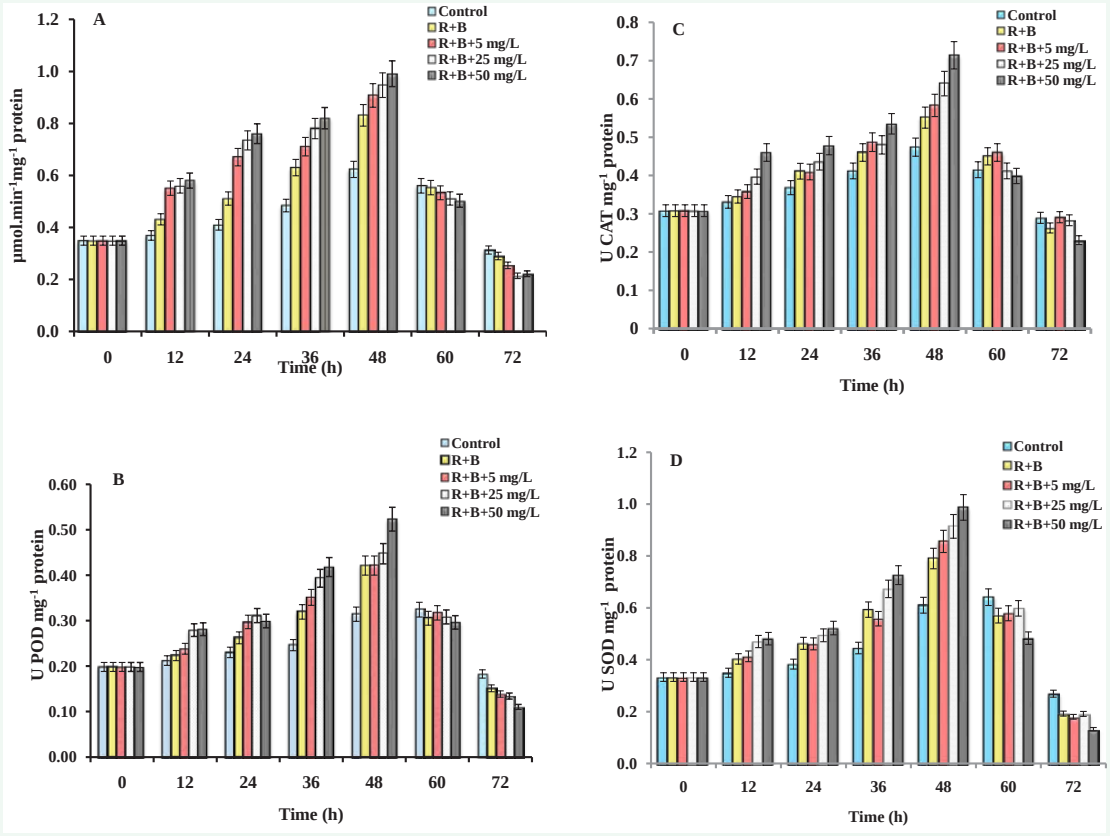

Figure 1 Activities of antioxidative enzymes in *Fischerella* sp. strain HKAR-5,under exposureof UV-B radiation, PAR and variable concentrationsof PA(0, 5, 25 and 50 mg/L) for varying duration of time. APX (A),POD (B), CAT (C) and SOD (D). Results are expressed as means of three replicates. Vertical bars indicate standard deviation of the means.

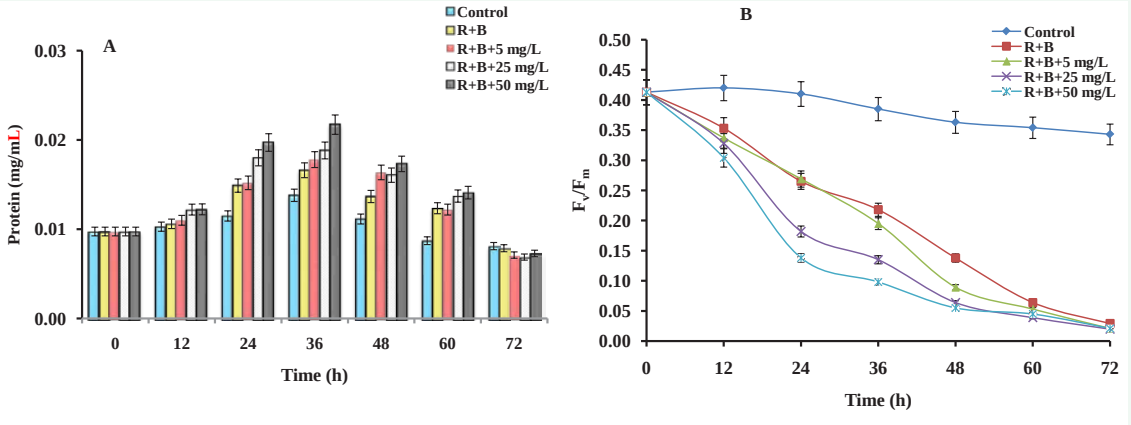

Figure 2 Combined effects of UV-B radiation, PAR and variable concentrations of PA (0, 5, 25 and 50 mg/L) on total protein (A) and photosynthetic activity of PSII (Fv/Fm) (B) in *Fischerella* sp. strain HKAR-5for varying duration of time. Results are expressed as means of three replicates. Vertical bars indicate standard deviation of the means.

CONCLUSION

The main aim of this work was to study the combined effects of PA, UV-B and PAR on the key physiological processes of the cyanobacterium *Fischerella* sp. strain HKAR-5, as not much information is available regarding such combined stressors. Deleterious effects of UVR on key physiological and biochemical processes of cyanobacteria have been well documented by several workers [10-15]. The naturally occurring polyphenolicallelo chemical PA is secreted by some aquatic vascular plants and exhibits strong inhibitory effects on harmful cyanobacteria; however, the mechanisms underlying this inhibitory effect are largely unknown.Detoxification of ROS produced during

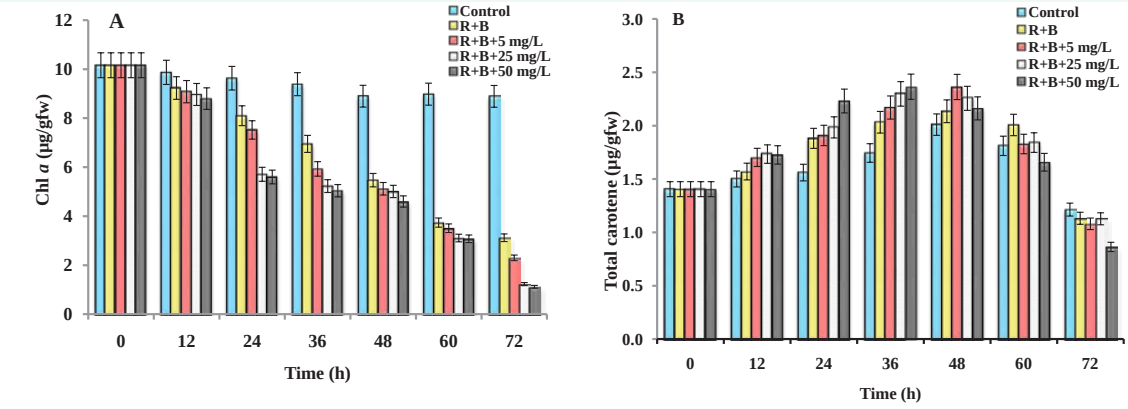

Figure 3 Combined effects of UV-B radiation, PAR and variable concentrationsof PA(0, 5, 25 and 50 mg/L) on photosyntheticpigments, Chl a (A) and total carotene (B) in *Fischerella* sp. strain HKAR-5for varying duration of time. Results are expressed as means of three replicates. Vertical bars indicate standard deviation of the means.

stresses, is usually achieved by use of enzymatic and non-enzymatic antioxidants such as carotenoids, ascorbate (vitamin C) or α-tocopherol, reduced glutathione, catalase or glutathione peroxidase and superoxide dismutase [32-35]. Under enzymatic antioxidant, ascorbate plays an important role in control of ROS by quenching it, generating α-tocopherol and acts as a substrate in both violaxanthin de-epoxidase and APX reactions.SOD is well known antioxidant enzyme present in the cell to inhibit the cellular damages from superoxide radicals. Superoxide (O_2^-), harmful by product of oxygen metabolism must be converted to harmless forms such as molecular oxygen or hydrogen peroxide. The hydrogen peroxide is further converted to water and O_2 via a combined catalase-peroxide system [35]. The mechanism of chemical reaction of SOD enzymes deals alternately by adding or removing an electron from the superoxide molecules. However, activities of other enzymatic antioxidants such as CAT, POD are more or less similar and this is very evident in the present investigation as all studied antioxidative enzymes (APX, POD, CAT and SOD) showed similar pattern of activity. Different abiotic stresses actively inhibit the photosynthetic efficiency of cyanobacteria. Photobleaching of photosynthetic pigments and disintegration of phycobilisome complex occur under UV-B radiation [7] along with triggering the de novo synthesis of D1 and D2 protein of photosystem II (PSII) [36]. The strength of effect of photosynthesis can be measured by analysing the value of F_v/F_m (photosynthetic activity of PSII), by using pulse amplitude modulation (PAM), evaluating the variable environmental conditions, different culture condition and ecophysiology of phytoplantons [37].

Recently few workers have investigated the mechanisms involved in the inhibitory effect of PAon cyanobacteria. PA induces the caspase-3(like)-dependent programmed cell death in the cyanobacterium *Microcystisaeruginosa* and exposure of 14 mg/L PA for 72 h to the cyanobacterium resulted in nucleoid disintegration, pyknosis formation, photosynthetic lamellae rupture, vacuolation and DNA fragmentation [31]. Lu et al. [38], studied the toxicity of PA on *Microcystisaeruginosa* and investigated generation of reactive oxygen species (ROS) as an end point. Exposure to 50 mg/L PA for 48 h caused the highest percentage of loss of membrane integrity (56.7%), and a 2.5 fold higher intracellular ROS level compared to control. Further investigation revealed that PA caused a dose-dependent increase in DNA strand breaks (DSB) of *M. aeruginosa* at exposure concentration from 2 to 50 mg/L [38]. Present investigation also showed similar response of the cyanobacterium as with increasing concentration of PA and duration of treatment of UV-B and PAR, protein content, pigmentation and photosynthetic efficiency decreased and maximum decrement was observed at 50 mg/L concentration of PA and at 72 h exposure of UV-B and PAR.In natural habitats cyanobacteria are exposed to multiple stresses at a time, hence studying combined stressors is more relevant as compared to individual stress and this motivated us to design this experiment. These combined stressors (such as PA+UV-B+PAR) cause severe damage to the physiology and metabolism of the cyanobacterium as evident by our results. These findings suggest that oxidative damage, photoreduction of photosynthetic pigments and photosynthesis inhibition are important modes of action for combined effect of variable concentration of PA and UV-B radiation with PAR on cyanobacterium *Fischerella* sp. strain HKAR-5.

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