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Photosynthetic performance of *Anabaena variabilis* PCC 7937 under simulated solar radiation

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Abstract

In vivo chlorophyll fluorescence analysis reflecting the photosystem II functionality was investigated in the cyanobacterium *Anabaena variabilis* PCC 7937 under simulated solar radiation in a combination with various cut-off filters (WG 280, WG 295, WG 305, WG 320, WG 335, WG 345, and GG 400) to assess the effects of photosynthetically active radiation (PAR), ultraviolet-A (UV-A), and ultraviolet-B (UV-B) radiations on photosynthesis. The photosynthetic activity (PA) was severely inhibited immediately after 10 min of exposure to high PAR, UV-A, and UV-B radiations compared with low PAR grown control samples. After 1 h of exposure, PA of 17.5 ± 2.9% was detected in the high PAR exposed samples compared with the control, while only a trace or no PA was observed in the presence of ultraviolet radiation (UVR). A recovery of PA was recorded after 2 h of the exposure, which continued for next 4, 8, 12, and 24 h. After 24 h of the exposure, PA of 57.5 ± 1.9%, 36.1 ± 11.7%, 23.5 ± 3.3%, 22.3 ± 5.2%, 20.8 ± 6.7%, 13.2 ± 6.6%, and 21.6 ± 9.5% was observed compared with the control sample in 400, 345, 335, 320, 305, 295, and 280 nm cut-off filters-covered samples, respectively. The relative electron transport rate, measured after 24 h exposure, showed also a disturbance in electron transfer between the two photosystems under the high PAR and UVR treatments relative to the control samples, suggesting the inhibition of photosynthesis. This study suggests that both high PAR and UVR inhibited the photosynthetic performance of *A. variabilis* PCC 7937 by damaging the photosynthetic apparatus, however, photoprotective mechanisms evolved by the organism allowed an immediate repair of ecologically important machinery, and enabled its survival.

Additional key words: cut-off filters; cyanobacteria; effective quantum yield of PSII; pulse amplitude modulated fluorometer; ultraviolet-B radiation.

Introduction

Cyanobacteria were the first organisms to release photosynthesis-dependent oxygen into the atmosphere by using water molecules as a hydrogen donor, and it resulted in the evolution of existing oxygen-dependent, aerobic life on the Earth (Fischer 2008). These Gram-negative prokaryotes are found in both terrestrial and aquatic ecosystems, and they perform ecologically important functions, such as photosynthesis and nitrogen fixation, to maintain the stability of ecosystems (Vaishampayan *et al.* 2001, Häder *et al.* 2011). Cyanobacteria are the major biomass producers in both fresh and marine aquatic ecosystems, and they also contribute significantly to the net productivity of terrestrial ecosystem (Häder *et al.* 2007). In addition, under nitrogen-limiting conditions, several cyanobacteria have inherent capacity to differentiate their vegetative cells into heterocyst, which can fix atmospheric nitrogen into ammonia, and thus increase the productivity of the nitrogen-deprived ecosystems (Zehr 2011).

Cyanobacteria are also a valuable source of pharma-

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Abbreviations: Car – carotenoids; Chl – chlorophyll; F_m' – maximal fluorescence yield of the light-adapted state; F_t – temporary fluorescence; MAA – mycosporine-like amino acid; PA – photosynthetic activity; PAR – photosynthetically active radiation; PBS – phycobilisome; PS – photosystem; rETR – relative electron transport rate; ROS – reactive oxygen species; UVR – ultraviolet radiation; Φ_{PSII} – effective quantum yield of PSII.

ceutically important compounds, and recently they have gained attention in space research and biofuel industry due to their resistance to several abiotic factors including a radiation and a high productivity per unit area (Rastogi and Sinha 2009, Cockell *et al.* 2011, Parmar *et al.* 2011). The successful utilization of cyanobacteria for human welfare depends upon two ecologically important processes, *i.e.*, photosynthesis and nitrogen fixation. Both photosynthesis and nitrogen fixation are energy-dependent processes and they require the harvesting of solar radiation. Cyanobacteria have evolved a light-harvesting complex that can gather the light from visible part of the solar spectrum, known as photosynthetically active radiation (PAR; 400 – 700 nm), to fuel both photosystem (PS) I and II. Their major light-harvesting complex, called phycobilisome (PBS), can harvest red or green light in red or green light enriched benthic environment to support the photosynthesis by fuelling the absorbed energy to the PS (Gutu and Kehoe 2012). Cyanobacteria have the ability to alter the pigment composition of PBS depending on the ambient light quality, and this ecologically important phenomenon is known as complementary chromatic adaptation (CCA) (Kehoe and Gutu 2006, Gutu and Kehoe 2012).

The rapid industrialization in the past few decades increased the level of chlorofluorocarbons in the stratosphere, which caused thinning of the ozone layer, and consequently resulted in a higher input of ultraviolet radiation (UVR; 280–400 nm) on the Earth's surface (Manney *et al.* 2011). The harvesting of PAR simultaneously exposes cyanobacteria to the lethal radiation of UVR, which is known to negatively affect the growth and survival of these organisms (Singh *et al.* 2010). UV-B (280–315 nm) can directly affect the genome and proteomes; however, its indirect effect involves the generation of reactive oxygen species (ROS) (Singh *et al.* 2010). The potentially toxic ROS can affect the survival of the organisms by oxidizing the lipid component of the biological membrane, DNA, and proteins (He and Häder 2002). Moreover, ROS is also known to damage the photosynthetic apparatus, consequently, resulting in the inhibition of photosynthesis (He and Häder 2002). Contrary to UV-B, UV-A (315–400 nm) can induce cell damage either by producing a secondary photoreaction of existing DNA photoproducts or *via* indirect, photosensitizing reactions (He and Häder 2002, Hargreaves *et al.* 2007). Recently, the generation of ROS and DNA strand break by UV-A in *A. variabilis* PCC 7937 was reported (Rastogi *et al.* 2010, 2011). However, under the selection pressure of both UV-B and UV-A radiations, cyanobacteria evolved and developed photorepair mechanisms, which utilize UV-A/blue light of the solar spectrum to repair the DNA lesions and photosynthetic machinery (Levine and Thiel 1987, Han *et al.* 2001, Rastogi *et al.* 2011).

UVR can cause photobleaching of the photosynthetic pigments, *e.g.*, chlorophyll (Chl), carotenoids (Car), and phycobiliproteins, and it was also found to destabilize the structure of PBS (reviewed in Singh *et al.* 2010). In addition, D1 and D2 proteins of PSII reaction centre have also been found to be degraded by UVR (Campbell *et al.* 1998). Although, several studies were performed to find out the damaging effects of UVR on photosynthetic components, reports related to the effects of UVR-induced damage on photosynthetic performance of cyanobacteria are limited. In the present investigation, we studied the photosynthetic performance of the cyanobacterium, *Anabaena variabilis* PCC 7937, using *in vivo* Chl fluorescence under a simulated solar radiation in the presence of series of cut-off filters, *i.e.*, WG 280, WG 295, WG 305, WG 320, WG 335, WG 345, and GG 400 to find out the consequence of UVR-induced damage on photosynthetic components.

Materials and methods

Experimental organism: *Anabaena variabilis* PCC 7937 was obtained from the Pasteur′s culture collection (*Institute Pasteur*, France). It is an autotrophically growing, heterocystous, and filamentous cyanobacterium. The cultures were routinely grown in a culture room at 20 ± 2°C with the continuous, fluorescent white light of 12 ± 2 W m^{-2} under axenic conditions in an autoclaved nitrogen-free Blue-Green Algae (BGA) liquid medium (Safferman and Morris 1964). All the experiments were performed using exponentially or logarithmically growing cultures having a total protein content of around 15 μg ml^{-1}.

Simulated solar radiation exposure: The cultures (in 3 replicates) were continuously exposed to a simulated solar radiation (*Sol 1200 W, mercury lamp 0383; Dr. Hönle,* Martinsried, Germany) in open cube black boxes (3 × 4 × 4 cm) from a height of 95 cm. The boxes were covered from the top with series of cut-off filters, *i.e.*, WG 280, WG 295, WG 305, WG 320, WG 335, WG 345, or GG 400 (*Schott Filter Series, Schott and Gen.,* Mainz, Germany) to get the desired radiation regimes. All experimental cultures were shaken regularly to avoid self-shading, and they were kept in a water bath at a constant temperature of *ca*. 23°C to avoid excess heating of the cells during irradiation. Fig. 1*A* shows the spectral irradiance of the solar simulator as measured with a double-monochromator spectroradiometer (*OL 754, Optronic Laboratories,* Orlando, FL, USA). The irradiances emitted from the solar simulator were 0.55 W m^{-2} for UV-B, 32.95 W m^{-2} for UV-A, and 134.73 W m^{-2} for PAR, while intensities effectively received by the samples are shown in Table 1, based on the transmission spectra of the cut-off filters used in this study (Fig. 1*B*). The culture, kept under the routine growth conditions as mentioned in the above section, was used as a control. Photosynthetic parameters were measured using *in vivo*

Table 1. Light intensities effectively received by the samples as transmitted by WG and GG series filters.

Filters	UV-B (280–315 nm) [W m^{-2}]	UV-A (315–400 nm) [W m^{-2}]	PAR (400–700 nm) [W m^{-2}]
WG 280	0.50	30.42	125.21
WG 295	0.41	29.88	122.93
WG 305	0.34	29.94	123.34
WG 320	0.00	29.56	122.28
WG 335	0.00	26.13	119.88
WG 345	0.00	21.67	116.35
GG 400	0.00	1.31	115.31

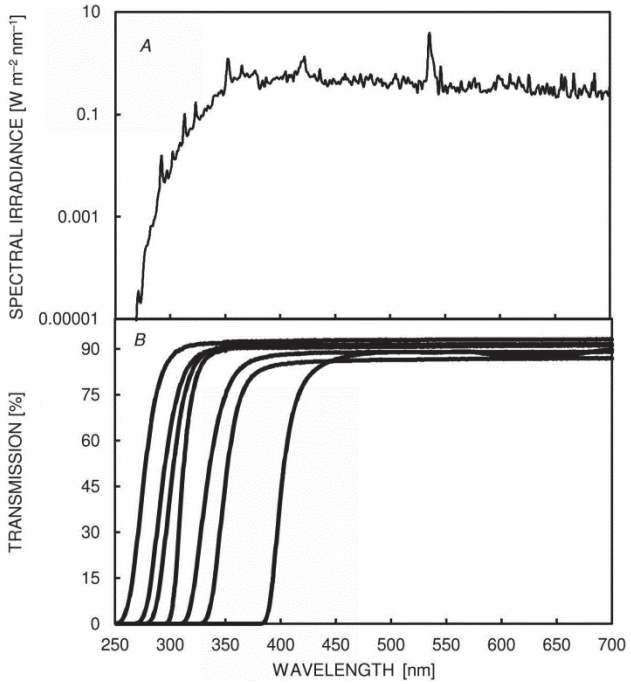

Fig. 1. Spectral characteristics of the solar simulator used in this study (*A*) and transmission spectra of different cut-off filters (from left to right WG 280, 295, 305, 320, 335, 345, and GG 400) used to cover *A. variabilis* PCC 7937 cultures during irradiation under simulated solar radiation (*B*). Y-axis in *A* is shown in logarithmic scale.

Chl fluorescence by means of a pulse amplitude modulated fluorometer (*PAM 2000, Walz,* Effeltrich, Germany). The PAM measurement is principally based on the change in Chl *a* fluorescence level after the application of an intense saturated light pulse, from which the effective quantum yield of PSII (Φ_{PSII}) can be calculated (Schreiber *et al.* 1994). The fiberoptics of PAM instrument was fixed at a distance of 2 mm from the surface of a sample, and a saturated light pulse (3500 μmol m^{-2} s^{-1} for 0.8 s) was applied to achieve the maximal fluorescence after the saturation of the photosynthetic electron transport chain. For Φ_{PSII} measurement, 1 ml of cell culture was withdrawn in a polystyrene VIS-cuvette, and the measurement was done immediately (no dark adaptation) for each of cut-off filters-covered samples after 10 min, 30 min, 1, 2, 4, 8, 12, and 24 h of the exposure to the simulated solar radiation. Φ_{PSII} was determined according to the following equation: $\Phi_{PSII} = (F_m' - F_t)/F_m'$, where F_m' represents maximal fluorescence yield of the light-adapted state, and F_t represents temporary fluorescence obtained immediately after switching on the measuring light (Genty *et al.* 1989). The relative electron transport rate (rETR) from different cut-off filters-covered samples was measured after 24 h of irradiation according to Rascher *et al.* (2003), which involved a determination of fluorescence at different irradiances of actinic light (0, 49, 89, 159, 259, 409, 589, 959; 1,399; and 2,099 μmol m^{-2} s^{-1}), generated by an internal halogen lamp. After a sample collection and before rETR measurement, the cultures were first incubated in the dark for 20 min in order to keep the primary electron acceptors in an oxidized state. The rETR was calculated as: rETR = maximal quantum yield of PSII × irradiance × 0.5, where 0.5 is a factor that accounts for the partitioning of energy between PSII and PSI. The absorptance of the cell suspension was not calculated in this study, and the light absorption fraction, *i.e.*, 0.84, generally used for leaves, was not included in the ETR calculations. Therefore, the term rETR was used.

Statistical analysis: All results were shown as a mean value of 2 measurements from 3 independent replicates (n = 6). All data were analysed by one-way *ANOVA*, and once a significant difference was detected, post-hoc multiple comparisons were made by using *Tukey*'s test. The significance level (α) was set at 0.05 for all tests (Brown 2005).

Results

Results from Φ_{PSII} measurements of *A. variabilis* PCC 7937 are shown in Fig. 2. The Φ_{PSII} decreased significantly immediately after 10 min of the exposure to the simulated solar radiation in all treatments in comparison with the control sample. However, Φ_{PSII} was the least affected in 400 nm cut-off filter (PAR-only)-covered

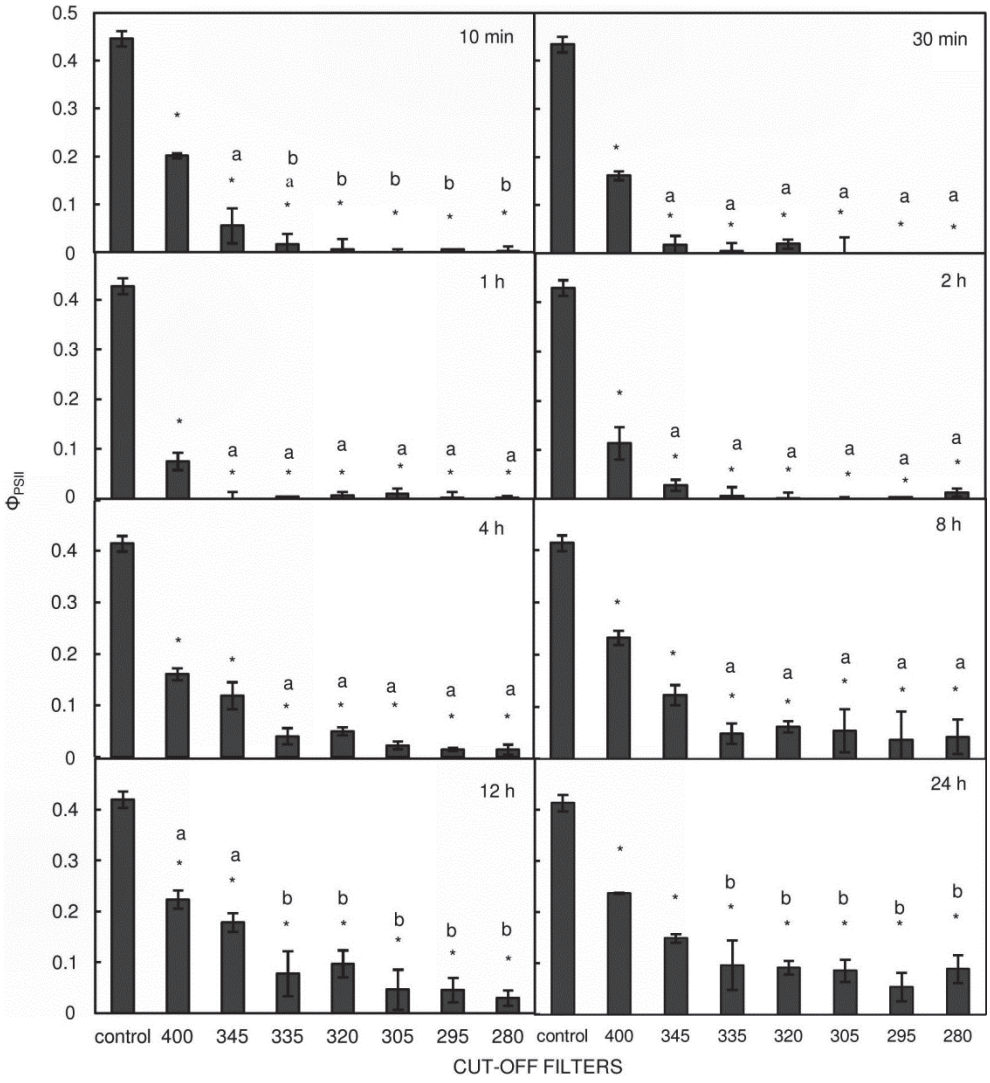

Fig. 2. Effective quantum yield of PSII (Φ_{PSII}) obtained after irradiation of *A. variabilis* PCC 7937 for different time intervals to simulated solar radiation in presence of different cut-off filters. * – significant difference from control sample (p<0.05); *similar letters* over bars represent homogenous mean groups (p>0.05). The sample grown under low PAR (12 W m^{-2}) was used as a control. Error bars indicate ± SD (n = 6).

Table 2. Percentage of effective quantum yield of PSII (± SD; n = 6) (compared with a control sample = 100%) detected at varying time intervals in different cut-off filters-covered samples after exposure to simulated solar radiation. * – significant difference from control sample in each column (p<0.05), while *numerals* and *letters* represent homogenous mean groups (p>0.05) within rows and columns, respectively.

Time	400 nm	345 nm	335 nm	320 nm	305 nm	295 nm	280 nm
10 min	45.18 ± 8.44^{*1,3}	12.48 ± 4.97^{*a1,2}	3.83 ± 4.84^{*ab1}	1.42 ± 1.44^{*b1}	0.00 ± 0.00^{*b1}	1.36 ± 2.35^{*b1}	0.45 ± 0.78^{*b1}
30 min	37.23 ± 5.07^{*1,2}	3.98 ± 3.79^{*a1}	1.23 ± 2.13^{*a1}	4.63 ± 8.01^{*a1}	0.00 ± 0.00^{*a1}	0.00 ± 0.00^{*a1}	0.00 ± 0.00^{*a1}
1 h	17.54 ± 2.89*	0.00 ± 0.00^{*a1}	0.89 ± 1.55^{*a1}	1.53 ± 2.65^{*a1}	2.27 ± 2.85^{*a1}	0.48 ± 0.84^{*a1}	0.48 ± 0.84^{*a1}
2 h	26.67 ± 3.98^{*2,4}	6.84 ± 4.86^{*a1}	1.55 ± 2.69^{*a1}	0.59 ± 1.02^{*a1}	0.00 ± 0.00^{*a1}	1.18 ± 2.04^{*a1}	2.92 ± 3.74^{*a1}
4 h	38.71 ± 5.87^{*1,4,5}	28.78 ± 4.49^{*2,3}	9.69 ± 2.20^{*a1,2}	12.00 ± 2.02^{*a1,2}	5.38 ± 0.66^{*a1}	3.52 ± 2.22^{*a1}	3.42 ± 3.09^{*a1}
8 h	56.29 ± 5.42^{*3}	29.82 ± 5.82^{*2,3}	12.03 ± 4.89^{*a1,3}	15.13 ± 3.20^{*a1,2}	13.42 ± 10.62^{*a1,2}	9.41 ± 13.75^{*a1}	10.50 ± 7.97^{*a1,2}
12 h	53.41 ± 5.80^{*a3,5}	42.64 ± 10.75^{*a3}	18.64 ± 6.96^{*b2,3,4}	23.44 ± 10.49^{*b2}	11.19 ± 6.33^{*b1,2}	12.01 ± 2.90^{*b1}	8.10 ± 6.98^{*b1,2}
24 h	57.45 ± 1.92^{*3}	36.12 ± 11.67^{*3}	23.46 ± 3.33^{*b4}	22.31 ± 5.20^{*b2}	20.78 ± 6.67^{*b2}	13.20 ± 6.63^{*b1}	21.60 ± 9.50^{*b2}

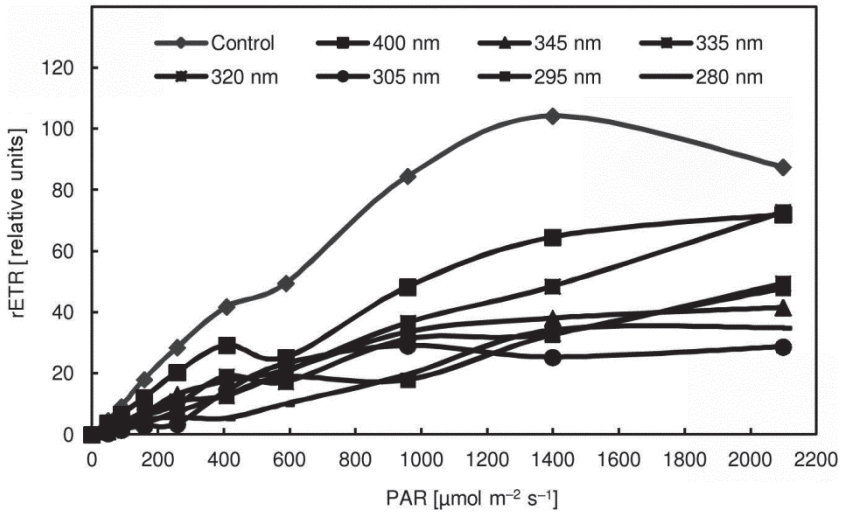

Fig. 3. The relative electron transport rate (rETR) of *A. variabilis* PCC 7937 from different cut-off filters-covered samples measured after 24 h of exposure to simulated solar radiation. The sample grown under low PAR (12 W m^{-2}) was used as a control.

sample, followed by 345 and 335 nm samples, where Φ_{PSII} was found to be the same after 10 min of the exposure. After the same time of the exposure, Φ_{PSII} was severely affected in 320, 305, 295, and 280 nm samples. There was no significant difference among 335, 320, 305, 295, and 280 nm samples after 10 min of irradiation. The further decrease in Φ_{PSII} was found in 400 nm sample in comparison with the control sample after 30 min of the exposure. However, Φ_{PSII} was found to be significantly higher in 400 nm sample in comparison with other cut-off filters-covered samples after the same time of the exposure.

The Φ_{PSII} was severely affected in 345, 335, 320, 305, 295, and 280 nm samples, where no or a trace level of photosynthetic activity (PA) was detected after 30 min of the exposure. The same trend was observed after 1 h of the exposure, when PA was seen only in 400 nm sample; however, Φ_{PSII} was significantly lower than the control sample. A recovery in photosynthetic machinery was seen in all samples except 320 and 305 nm samples after 2 h of the irradiation However, Φ_{PSII} was significantly lower than the control sample in all samples, and Φ_{PSII} was found to be highest in 400 nm sample in comparison with other cut-off samples. There was no significant difference in Φ_{PSII} among 345, 335, 320, 305, 295, or 280 nm samples. PA was detected in all samples after 4 h of irradiation, when Φ_{PSII} was found to be highest in 400 nm samples, but still significantly lower than the control sample, followed by the 345 nm samples. There was no significant difference in Φ_{PSII} among 335, 320, 305, 295, or 280 nm samples. Similarly, Φ_{PSII} was found to increase further in all cut-off filters-covered samples after 8 h of irradiation, and the trend was the same as obtained after 4 h of the irradiation. Φ_{PSII} was found to be similar in 400 and 345 nm samples after 12 h of the exposure; however, it was significantly lower than the control sample, and there was no significant difference among 335, 320, 305, 295, or 280 nm samples. Φ_{PSII} from all treatments were significantly lower than in the control sample after 24 h of the exposure, however, Φ_{PSII} was found to be highest in 400 nm sample, followed by 345 nm sample in comparison with other treatments. There was no difference among 335, 320, 305, 295, and 280 nm samples after the same duration of the exposure.

Table 2 represents percentage of Φ_{PSII} in different cut-off filters-covered samples at varying time intervals compared with the control sample. The Φ_{PSII} was inhibited by more than 50% in 400 nm sample immediately after 10 min of the irradiation, while only 12.5% PA was detected in 345 nm sample. In other cut-off filters-covered samples, Φ_{PSII} was found to be inhibited by more than 90% of the control sample after 10 min of exposure. Φ_{PSII} was found to be further inhibited after 30 min and 1 h of the exposure in all samples reaching 37.23 and 17.5%, respectively, of the control sample in 400 nm sample, while in other samples only trace level of PA was detected. During the next hour of exposure, a recovery was seen in all samples; and 57.5% PA of control sample was detected in 400 nm sample after 24 h of the exposure. Similarly, after 24 h of the exposure, 36.1, 23.5, 22.3, 20.8, 13.2 and 21.6% PA was seen n 345, 335, 320, 305, 295, and 280 nm samples, respectively.

rETR increased with the increase in the irradiation until it reached a saturation point, and rETR values were found to be lower from all cut-off filters-covered samples than the control sample (Fig. 3). rETR was highest in the sample receiving only PAR; however, in other samples receiving PAR+UV-A+UV-B, rETR values were lower. Thus, it was clear that even higher level of PAR inhibited the photosynthesis in *A. variabilis* PCC 7937, and presence of UV-A and UV-B radiation further augmented this process.

Discussion

Cyanobacteria are photoautotrophic organisms and their growth and survival is regulated by both quantity and quality of the prevailing light conditions in their natural habitats (Singh *et al.* 2010). Cyanobacteria have evolved their genome in such a way that they can sense the change in ambient light conditions, and they can adapt their photosynthetic machinery accordingly (Los *et al.* 2010). The photosynthetic performance of the cyanobacterium was found to be adversely affected even in PAR-only treatment in comparison with the control sample immediately after the exposure, which could be explained by the fact that these samples were adapted to a low light (12 W m^{-2}) condition before the start of the experiment, and a sudden transfer to high light intensity (134.73 W m^{-2}) probably resulted in a damage in photosynthetic apparatus (Bhandari and Sharma 2006).

In this study, low-PAR-adapted cells were directly transferred to high PAR or high PAR+UVR, which was contrary to the natural conditions, where the light intensity increases gradually reaching the maximum at noon, and therefore, it allows cells to adapt to the changing irradiation. Moreover, the ratio of UV-B:UV-A:PAR obtained from the solar simulator was different from that observed in the nature. Hence, one should take care of the data interpretation. The observed decrease in PA in the presence of high PAR was in accordance with earlier reports, where high irradiance of PAR decreased the photosynthesis in a dose-dependent manner, and resulted in a lower photosynthesis-dependent oxygen evolution (Bhandari and Sharma 2006; Wu *et al.* 2005). The growth of *A. variabilis* PCC 7937 was inhibited by UVR, which could also be due to the decrease in photosynthesis, similarly observed in this study, in addition to the DNA damage and oxidative stress reported earlier (Rastogi *et al.* 2011).

The high intensity of PAR interferes with the transfer of excitation energy to PS, and also damages the photosynthetic reaction centers, which consequently results in a reduced photosynthetic performance of the organism (Bhandari and Sharma 2006). Absorption of excess energy also leads to the production of ROS, which affects the PA of cyanobacteria by damaging the lipid content of membrane, proteins, genomic DNA, and bleaching the photosynthetic pigments (He and Häder 2002, Bhandari and Sharma 2006, Rastogi *et al.* 2010). The acclimatization of *Trichodesmium* sp. to high light involved a change in cellular morphology to reduce the exposed surface, to increase protein turnover, to lower Chl content, and to change PBS structure and its attachment to the reaction centres (Andresen *et al.* 2010). Cyanobacteria have also the ability to quench the excess energy from PBS by orange Car protein, and they can dissipate this excess energy as heat in nonphotochemical quenching, which prevents the damage of reaction centre by inhibition of the transfer of the excess energy from PBS (Gorbunov *et al.* 2011).

UVR is the very small proportion of total radiation reaching the Earth's surface, however, this part of solar spectrum is highly energetic in comparison to PAR, and known to affect the morphology, cell differentiation, survival, growth, pigmentation, motility and orientation, N_2 metabolism, phycobiliprotein composition, protein profile, DNA, and CO_2 uptake in cyanobacteria (Kirk 1994, Singh *et al.* 2010). The photosynthetic performance of *A. variabilis* PCC 7937 was severely affected immediately after 10 min of the exposure to UVR, however, PA was significantly higher in the samples receiving only UV-A radiation in comparison to the UV-B exposed samples. This can be explained by the fact that within UVR, photons of UV-B region are highly energetic compared to photons of UV-A region, and this excess energy can damage the photosynthetic machinery and other biomolecules. The UV-B radiation is known to decrease the phycobiliprotein content, and it also causes a disassembly of the phycobilisomal complex in cyanobacteria (Sinha *et al.* 1995, 1997). Exposure of cyanobacterial cultures to UV-B radiation causes bleaching of phycocyanin and phycoerythrin (Sinha *et al.* 2005). Furthermore, the fluorescence emission spectra of phycobiliproteins following UV-B irradiation suggested an impairment of the energy transfer from the accessory pigments to the photosynthetic reaction centre, supporting the earlier inhibition of PA in this study (Sinha *et al.* 1995, 1997).

UV-B radiation was found to damage αβ monomers of phycocyanin and linker polypeptides of cyanobacterial PBS after 1 h of irradiation (Sinha and Häder 2003). The PA was severely inhibited by both UV-A and UV-B radiation, however, higher wavelengths of UV-A had a lesser inhibitory effect on photosynthesis than the lower ones of the UV-A and UV-B regions. Also, the wavelength-independent effect on photosynthesis was seen in the presence of UVR, and both UV-A and UV-B affected the photosynthesis in a similar way. UVR also negatively affects the ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity in cyanobacteria, in addition to damaging the light-harvesting complex (Sinha *et al.* 2008). The D1 and D2 proteins, major constituents of PSII reaction centres, were also shown to be damaged after exposure to even intermediate levels of UV-B radiation (Sass *et al.* 1997, Campbell *et al.* 1998). Several families of transcripts, including mRNAs-encoding proteins involved in light harvesting and photosynthesis, were also reported as downregulated by UV-B treatment, suggesting a reduced PA following UV-B exposure (Huang *et al.* 2002).

The damage caused by both high PAR and UVR was reversible, and recovery in PA of *A. variabilis* PCC 7937

was seen after 2 h of irradiation in all treatments. However, the recovery was low in the presence of UVR, which could be due to its higher damaging effects on the cell. Cyanobacteria have evolved several mitigation strategies to keep their photosynthetic machinery working. They increase the turnover of D1 and D2 proteins of the PSII reaction center, when exposed to UV-B radiation (Sass *et al.* 1997). *Synechococcus* sp. PCC 7942 changed the expression of *psbA* family genes (*psbAI, psbAII and psbAIII*), encoding D1 proteins of PSII, within 15 min of UV-B exposure, and accumulated higher level of psbAII and psbAIII transcripts (Campbell *et al.* 1998). A mutant strain of *Synechococcus* sp. PCC 7942, expressing only *psbAI*, was found to be sensitive to UV-B radiation with PA inhibited in comparison to one that was constitutively expressing *psbAII* and *psbAIII* genes (Campbell *et al.* 1998).

Instant turnover of PSII reaction center proteins helps during the acclimatization, and it provides a resistance against UVR in cyanobacteria. Cyanobacteria also synthesize photoprotective compounds, such as mycosporine-like amino acids (MAAs) and scytonemins, and colonies of *Nostoc flagelliforme*, containing a higher concentration of glycosylated MAAs and scytonemin, were more resistant to UVR in terms of PA measured by PAM (Ferroni *et al.* 2010, Singh *et al.* 2010). *A. variabilis* PCC 7937 also synthesizes a single MAA shinorine, having absorption maximum at 334 nm, which could be possibly involved in the photoprotection against UV-A radiation (Singh *et al.* 2008). MAAs also provide a protection against ROS, and glycosylated MAAs from *Nostoc commune* contributed by 27% of the total radical scavenging activities *in vitro* (Matsui *et al.* 2011). In nature, *Anabaena* strains are found in shallow water habitats, where they receive intense PAR and UVR. However, mitigation strategies evolved by these organisms, such as UV absorption by MAAs, ROS detoxification by enzymatic and nonenzymatic antioxidant systems, as well as photorepair of DNA lesions and photosynthetic machinery, support their survival after the exposure to intense PAR and UVR in their brightly lit habitats.

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