Effects of Algal Utilization of Dissolved Organic Phosphorus by *Microcystis Aeruginosa* on its Adaptation Capability to Ambient Ultraviolet Radiation

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Abstract

Phosphorus (P) plays an important role in eutrophication and algal adaptation to environmental stresses; therefore, a better understanding of the impact of P is essential to control cyanobacterial bloom. In this study, *Microcystis aeruginosa* was treated with 5-h of ambient irradiation in the culture medium with different availability of dissolved organic P (DOP) and dissolved organic matter (DOM), to explore algal responses. Compared to photosynthetically active radiation (PAR), ambient UV-A and UV-B radiation exerted oxidative stresses and had inhibitive effects on the growth and photosynthesis of *M. aeruginosa* in DOP-rich medium. However, *M. aeruginosa* had a strong adaptation capability and the negative effects of UV radiation were eliminated with DOM addition (5 mg L⁻¹ humic acid [HA]). Combining dissolved inorganic P (DIP) and DOP contents in the culture medium, adaptation of *M. aeruginosa* to UV radiation in the DOP-rich waters could be mainly achieved through the hydrolysis of DOP and metabolism of DIP, and the DOP utilization behaviors of *M. aeruginosa* greatly affected its UV adaptation capability. In DOP-rich medium without DOM, APase inactivation after UV radiation negatively affected DOP utilization by *M. aeruginosa*, and algal P demand for UV adaptation could not be fully met. DOM could act as an antioxidant and greatly decreased APase inactivation after UV radiation, when *M. aeruginosa* utilized DOP faster to produce more DIP and to increase algal carotenoid, phycocyanin production and its superoxide dismutase (SOD) activity in the DOP-rich medium, resulting in a strong UV adaptation capability. Consequently, *M. aeruginosa* showed the lowest adaptation capability to UV radiation in the DOP-free medium. Overall, our findings indicated the close relationship of algal DOP utilization and its adaptation to ambient UV radiation of typical cyanobacteria in DIP-limited and DOP-enriched natural waters.

1. Introduction

Eutrophication is a significant threat to aquatic ecosystems globally and harmful algal blooms (HABs) are a troubling indicator of accelerating eutrophication, which could adversely affect water quality and sustainability of impacted systems (Carey et al. 2012; Paerl et al. 2011). For a long time, cyanobacteria ranked prominently among causes of problems with HABs from the environmental degradation and human health perspectives (Ni et al. 2019; Huisman et al. 2018). Consequently, studies have focused on the growth patterns and physiology of *Microcystis* in recent years, which is one of the dominant cyanobacterial genus in natural waters and can produce many secondary metabolites such as microcystins (Wang et al. 2015). Results showed that, *Microcystis* has developed a range of adaptations to defend against complex environmental stresses (Davis et al. 2009; Paerl 2014; Xu et al. 2019), which are vital for its proliferation.

In all kinds of environmental stresses, light could directly affect the photosynthesis and growth of cyanobacteria (Wu et al. 2009; Wang et al. 2015), which highly depended on the intensity, exposure time and wavelength of light radiation. For example, other than photosynthetically active radiation (PAR; 400–700 nm), increased solar ultraviolet (UV) radiation is reaching earth surface as a consequence of serious stratospheric ozone depletion and other factors (Hader et al. 2015; Carrillo et al. 2008). In recent years,

effects of UV radiation on phytoplankton have received considerable attention and most studies have used *Microcystis* as a model species (Beardall et al. 2014; Xu et al. 2019). For example, the extracellular polysaccharides (EPS) of *Microcystis* could facilitate the aggregation of algal cells (Chen et al. 2019), which was helpful to reduce the exposure and negative effects of UV radiation (Gan et al. 2012). The synthesis of microcystin by *Microcystis* could contribute to a higher fitness of cells under enhanced light irradiation through a covalent interaction with the cysteine residue of proteins (Zilliges et al. 2011). Results indicated that adaptation of cyanobacteria to UV radiation was a complicated process, but many studies used enhanced UV radiation rather than ambient irradiance in natural waters (Rath and Adhikary 2007; Sakai et al. 2007). Moreover, less attention was paid on the effects of macro-nutrient content and other common substances in water on UV adaptation capability of typical cyanobacterial species.

Phosphorus (P) is an essential macro-nutrient for algae and the important roles of P for algal growth has been extensively studied. It was indicated that P availability could influence the physiological processes and adaptation of cyanobacteria to environmental stresses (Shi et al. 2003; Carrillo et al. 2015). For example, higher dissolved inorganic P (DIP, mainly as phosphate) in water could enhance algal production of photosynthetic pigments and the antioxidase activity of UV-radiated *M. aeruginosa*, leading to a higher adaptation capability (Ren et al. 2020). However, DIP shortage has become a common phenomenon in many systems and algae often produced alkaline phosphatase (APase) to hydrolyze dissolved organic P (DOP) for phosphate in the natural waters, which was an indirect process for algal P utilization (Ma et al. 2019) and might result in different manners for the adaptation of cyanobacteria to UV radiation. Especially, regions at mid-low latitudes are more threatened by UV radiation (Morris et al. 1995) and *Microcystis* often occur as surface blooms, which are assumed to be more negatively influenced by UV radiation. However, the frequency and intensity of *Microcystis* blooms maintained high levels in eutrophic lakes, and it is crucial to study the adaptation of *Microcystis* to UV radiation in the medium with DOP. Moreover, APase was sensitive to UV radiation (Scully et al. 2003; Hessen et al. 2012) and inactivation of APase might affect the DOP utilization by *Microcystis*, but there are few relevant studies.

Meanwhile, high contents of dissolved organic matter (DOM) exist in the natural waters, which originate from microbial decomposition of organisms and the terrestrial environment (Murphy et al. 2008; Zhang et al. 2009). It has been reported that DOM could absorb photons and encounter many reactions. For example, light attenuation by DOM often happened but photo-oxidation of DOM could also produce reactive oxygen species (ROS), resulting to different influences on APase (Zhang et al. 2011; Janssen et al. 2014). However, these results are often contradictory and effects of DOM on algal utilization of DOP should gain considerable attention.

In this study, we select *M. aeruginosa* and investigate its physiological responses after short-term irradiation in the culture medium with different availability of DOP and DOM. The main aims were to: (i) analyze the effects of UV radiation on the growth and photosynthesis of *M. aeruginosa*, (ii) explore the relationships of algal UV adaptation capability with its DOP utilization behavior.

2. Materials And Methods

2.1. Preparation of algae cultures and DOM solution

A common unicellular bloom-forming cyanobacteria (*M. aeruginosa* FACHB 905) was selected and obtained from the Freshwater Algae Culture Collection of the Institute of Hydrobiology, Chinese Academy of Sciences (FACHB). The detailed procedures for inoculation and enlarge cultivation of *M. aeruginosa* can be seen in Ren et al. (2017). Cell density was monitored until it exceeded 2.0×10^7 cells mL⁻¹, after which cells were harvested by centrifugation (5000 *g* for 10 min, 4°C), washed with ultrapure water and suspended in P-free BG₁₁ medium for our experiment.

Since humic substances can occur from plant or animal remains through biological or chemical transformations and are known as the main pool of DOM (Canellas et al. 2015), DOM solution was obtained using humic acids (HA) from Sigma-Aldrich in our study. HA was dissolved in the ultrapure water at pH = 10.0 and ultrasonic treatment was conducted intermittently until pH remained stable. Then, the solutions were adjusted to pH = 7.0, filtered (0.2-μm, Whatman) and preserved in dark place at low temperatures. The total organic carbon (TOC) content of DOM stock solution was 150.0 mg L⁻¹ using a TOC analyzer (Shimadzu, Japan).

2.2. Experimental setup

2.2.1 Effects of irradiation on *M. aeruginosa*

The prepared *M. aeruginosa* was collected by centrifugation (5000 *g* for 10 min, 4°C) and transferred into two different culture media (DOP-rich medium and DOP-free BG₁₁ medium). The composition of DOP-rich medium was identical to standard BG₁₁ medium except for replacing dipotassium phosphate with glucose-6-phosphate, which is a common form of DOP in the natural waters (Bai et al. 2009; Table S1). Based on P concentrations in many aquatic ecosystems and our previous research (Ren et al. 2020), a high level of DOP was adopted (2.5 mg L⁻¹) in DOP-rich medium. Then, DOM stock solution were added into half the petri dishes at a final content of 5.0 mg TOC L⁻¹, representing four experimental groups: without DOM in DOP-rich medium (NM-P group), with DOM in DOP-rich medium (M-P group), without DOM in DOP-free medium (NM-NP group), with DOM in DOP-free medium (M-NP group). The selected DOM availability in our experiment could reflect its ambient concentrations during the outbreak period of HABs (Ren et al. 2015; Boyer et al. 2006).

Then, the cultures were transferred into sterilized petri dishes for 5-h of PAR, UV-A and UV-B irradiation exposure. The irradiation intensity for PAR was 70 W m⁻² and the narrowband UV-A and UV-B lamps were used with the weighted radiation intensity of about 30 and 1.0 W m⁻², respectively, which was close to that in the natural aquatic ecosystems (Fig. S1-S3). Considering that intensities of UV radiation in the field often exhibited dynamic hourly values (Fig. S4) and the main goal of our study was to explore the UV adaptation mechanisms of *M. aeruginosa*, algal cultures in the petri dishes were immediately returned

to flasks and incubated under $40 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ PAR for 10 days for recovery after irradiation treatment. Therefore, the experimental conditions could somewhat replicate the ambient light exposure on *M. aeruginosa* in natural waters.

According to our preliminary experiment, glucose-6-phosphate could maintain its stability and did not decompose significantly with 5-h PAR, UV-A, or UV-B radiation with the same intensities in our study (Fig. S5). A schematic diagram of experiment is shown in Fig. S6 and the details could be seen in SI.

2.2.2 Effects of irradiation on APase inactivation

The exponentially growing *M. aeruginosa* cells were harvested by centrifugation (5,000 g for 10 min, 4°C) and suspended in the Tris-HCl buffer (20 mmol L^{-1} , pH 8.2). Then, cells were disrupted for 15 minutes with the sonication in an ultrasonic pulverizer (1200-98, BioSafer, China) cooled with an ice bath. The slurry was filtered through 2.0- μm filters (Whatman) and the filtrate was centrifuged at 6,000 g for 10 min (4°C). The supernatant was immediately mixed with ultrapure water (Millipore) to create enzyme samples containing *M. aeruginosa* APase with initial APA of $2.0 \mu\text{mol L}^{-1}$.

Enzyme solution was prepared in petri dishes (5 cm in diameter, 20 mL of volume) and DOM solution was added into half the dishes ($5.0 \text{ mg TOC L}^{-1}$). Then, petri dishes were subjected to irradiation for 5-h, when the intensity and operating methods of PAR, UV-A or UV-B treatments were the same as mentioned above. Meanwhile, petri dishes were placed in a sterile dark tank for comparison. Aliquots were regularly taken from the dishes for APA determination.

Details of our experiment were shown in SI.

2.3. Analytical methods

2.3.1 Cell density and photosynthetic efficiency

The subsamples were taken immediately after irradiation treatment and every two days for determining the cell density. Meanwhile, a Phyto-PAM fluorometer (Hein Walz, Germany) was used to determine the effective quantum yield (F_v/F_m) of *M. aeruginosa* (Campbell et al. 1998; Wang et al. 2010). The detailed procedures were shown in SI.

2.3.2 Contents of photosynthetic pigments

At the beginning and after 5-h of light exposure, a subsample of algal cultures was collected to determine the contents of photosynthetic pigments in single cells, including chlorophyll a (Chl-a), carotenoid (CAR), and phycocyanin (PC). Details can be seen in SI.

2.3.3 ROS and antioxidant responses

Before and after light exposure, the generation of ROS by *M. aeruginosa* and the activity of superoxide dismutase (SOD) were determined. Details can be seen in SI.

2.3.4 Kinetic parameters of DOP uptake

At the beginning and after light exposure, the kinetic parameters of DOP uptake by *M. aeruginosa* were determined to investigate the combined effects of the irradiation treatments and DOM addition. The methods were modified from Fu et al. (2006) and details can be seen in SI.

2.3.5 P fractions and cellular P quota

Based on inductively coupled plasma (ICP) method, DOP and DIP concentrations in the culture medium was measured. Meanwhile, the total amount of P associated with *M. aeruginosa* cells was determined and the cellular P quota was estimated (pg cell^{-1}). Detailed methods can be seen in Ren et al. (2020).

2.3.6 Morphology of algae cells

To explore the microstructure of *M. aeruginosa* after radiation, scanning electron microscopy (SEM) analysis was conducted on Day 1, when algae cells were collected by centrifugation (5000 g for 10 min, 4°C) and fixed with 2.5% glutaraldehyde solution for 24-h. After rinsing with phosphate buffer solution (PBS), cells were dehydrated successively by a series of ethanol solutions in a vacuum drier (50%, 70%, 90% and 100%). Subsequently, the treated cells were mounted on copper stubs, coated with spray gold, and examined through a SEM (S-4800, Hitachi, Japan) at 5 kV.

2.3.7 Estimation of APA and its inactivation rates

After regular collection of algal cultures or enzyme solutions, APA was estimated using *p*-nitrophenylphosphate (*p*NPP) as the substrate (Ren et al. 2015).

The inactivation rates of APase (K_{ina}) was calculated as follows: $K_{ina} = (\ln \text{APA}_t - \ln \text{APA}_0)/T$, where APA_t and APA_0 are the measured APA and initial APA, respectively, and T was the irradiation time (Janssen et al. 2014).

2.4. Statistical analysis

All experiments were conducted in triplicate and means $\pm$ standard deviations of three replicates were calculated. The parametric three-way repeated-measures analysis of variance (RM-ANOVA) was used to determine the effects of irradiation treatments, DOM and sampling time on the cell density, photosynthetic parameters, cellular P quota, APA of algal samples and the inactivation of APase. Meanwhile, two-way RM-ANOVA was used to determine the effects of irradiation and DOM on photosynthetic pigments, ROS, algal SOD activity, and DOP uptake rates. Data were tested for normality and the variance assumptions of parametric ANOVA, and no data transformation was needed. If the interaction factor was significant at $p < 0.05$, a one-way ANOVA followed by Tukey's test was adopted to determine where differences lie. All statistical analyses were performed using SPSS 22.0 (Chicago, IL, USA).

3. Results

3.1. Effects on the growth of *M. aeruginosa*

In our previous study (Fig. 1a and 1b; Ren et al. 2020), higher P availability in the water alleviated the negative effects of UV radiation on algal growth, leading to a better adaption capability of *M. aeruginosa*. Similarly, cell density of *M. aeruginosa* did not change significantly ($p > 0.05$) after short-term radiation, and differences in the growth of *M. aeruginosa* were evident during the recovery period in this study.

In NM-P group, *M. aeruginosa* grew persistently but the inhibition effect by UV radiation was significant after Day 2, which was largest in UV-B treatment ($p < 0.05$). Comparing to the results using DIP ((Fig. 1a and 1b), high DOP did not fully eliminate the negative effects of UV radiation on algal growth. In M-P group, the maximum cell density of *M. aeruginosa* in PAR was similar to that in NM-P group. Moreover, algal growth among three treatments were comparable ($p > 0.05$) during the incubation in M-P group, and no significant effects ($p > 0.05$) of UV radiation were observed.

However, in NM-NP and M-NP groups, *M. aeruginosa* both grew slowly in PAR treatment and UV radiation showed the significant negative effects ($p < 0.05$) on algal growth, when the impact was greater in UV-B treatment. Moreover, DOM addition did not significantly change the effects of irradiation on algal growth ($p > 0.05$).

3.2. Effects on algal photosynthetic efficiency

Comparing to PAR, 5 h of UV radiation might directly impair the normal function of algal photosynthetic system, and F_v/F_m of *M. aeruginosa* both declined significantly after UV radiation under different experimental conditions ($p < 0.05$; Fig. 2). However, the degree of decline and the recovery of F_v/F_m after withdrawing UV radiation showed a great difference in this study.

In NM-P group, F_v/F_m did not change obviously after PAR treatment, and F_v/F_m decreased by 58.2% and 78.2% after UV-A and UV-B radiation, respectively (Fig. 2a). Then, F_v/F_m increased to 74.5% and 63.6% of the initial value on Day 1 in UV-A and UV-B treatment, respectively, and the differences among treatments were not observed until Day 7. In M-P group, the decline of F_v/F_m decreased obviously after UV radiation, and F_v/F_m could recover and exceed 95% of the initial value on Day 1 (Fig. 2b). Then, F_v/F_m in three treatments were similar during the subsequent incubation.

Similar to the variation patterns of cell density, the decline degree of F_v/F_m did not differ significantly in NM-NP and M-NP groups after UV radiation ($p > 0.05$; Fig. 2c and 2d), when F_v/F_m decreased by about 70% and 90% after UV-A and UV-B radiation, respectively. However, F_v/F_m showed a decline in PAR treatment during the recovery period in NM-NP and M-NP groups, and it recovered to a certain extent and remained constant afterwards in UV-A and UV-B treatments. Moreover, the recovery of F_v/F_m and its variation patterns after withdrawing UV radiation did not differ significantly ($p > 0.05$) in NM-NP and M-NP groups.

3.3. Antioxidant responses and photosynthetic pigments

3.3.1 ROS production and SOD activity

Compared to the initial values, ROS production by *M. aeruginosa* and algal SOD activity changed slightly after PAR treatment in four groups ($p > 0.05$; Fig. 3a). But ROS production by *M. aeruginosa* was enhanced to varying degrees after UV-A or UV-B radiation, and it was higher ($p < 0.05$) in the DOP-free medium (NM-NP and M-NP groups). Moreover, two distinct effects of DOM addition on algal ROS production were observed in DOP-rich medium and DOP-free medium, which decreased greatly in M-P group and increased in M-NP group, respectively.

Consistent with algal ROS production, SOD activity of *M. aeruginosa* remained constant after PAR treatment and algae could increase SOD activity after UV radiation, which was higher in UV-B treatment ($p < 0.05$). In the DOP-rich medium, algal SOD activity greatly decreased with the addition of DOM (M-P group). But in the DOP-free medium, algal SOD activity increased obviously with DOM addition (M-NP group).

3.3.2 Photosynthetic pigments of *M. aeruginosa*

Chlorophyll-*a* in single cells did not change significantly after irradiation in both four groups ($p < 0.05$; Fig. 3), but increase of CAR and PC in single cells was observed after UV-A and UV-B radiation in NM-P and M-P groups, which was more pronounced in UV-B treatment. Meanwhile, the higher levels ($p < 0.05$) of CAR and PC appeared in M-P group, and CAR and PC contents in single cells only increased to a smaller degree in NM-P group. On the contrary, the evident decrease of CAR and PC in single cells was observed after UV radiation in NM-NP and M-NP groups, and DOM addition did not show significant effects ($p > 0.05$).

3.4. Surface morphology of cells

SEM images of *M. aeruginosa* on Day 1 showed that, the spherical shape of algal cells did not change greatly in both four groups, and cell surfaces were both glossy and intact after PAR treatment (Fig. 4). In NM-P group, the intact surfaces of cells were also observed in UV-A and UV-B treatments, and several evident wrinkles existed with clear boundaries. But in M-P group, the exterior morphology of algal cells in UV-A and UV-B treatments were fairly glossy, when cells with sharp edges were easy to distinguish. In NM-NP and M-NP groups, the most evident changes of algal cells after UV radiation were observed, when the surfaces were both shrunk and became rough.

3.5. DOP utilization behavior after irradiation

3.5.1 Kinetic parameters for DOP uptake

The kinetics parameters for DOP uptake by *M. aeruginosa* cells changed slightly after PAR exposure, and they were strongly affected by the availability of DOM and DOP after UV radiation (Table 1). In NM-P group, the significant drop of $V_{\max}$ ($p < 0.05$, 19.8%-34.2%) was observed and K_m increased markedly after UV radiation ($p < 0.05$), indicating the slower DOP uptake rate and the worse affinity to DOP. But in M-P

group, $V_{\max}$ increased ($p < 0.05$, 11.4%-22.4%) and K_m was less affected after UV radiation, indicating the faster DOP uptake rate and the better affinity to DOP.

Table 1
Kinetic parameters for DIP uptake by *M. aeruginosa* after 5 h of irradiation (* indicates a significant difference between treatments and the initial value at $p < 0.05$)

Experimental Groups	Irradiation Treatment	$V_{\max}$	K_m
		($\mu\text{g P mg}^{-1} \text{ DW}\cdot\text{h}^{-1}$)	($\mu\text{g P L}^{-1}$)
	<i>Initial value</i>	10.25 (± 0.08)	480.23 (± 5.40)
NM-P	PAR	10.30 (± 0.12)	474.48 (± 2.66)
	UV-A	8.22 (± 0.20)*	626.87 (± 5.63)*
	UV-B	6.75 (± 0.46)*	775.18 (± 13.03)*
M-P	PAR	10.24 (± 0.14)	465.82 (± 4.20)
	UV-A	11.42 (± 0.25)*	470.30 (± 5.29)
	UV-B	12.55 (± 0.21)*	473.20 (± 4.69)
NM-NP	PAR	10.24 (± 0.09)	485.52 (± 3.24)
	UV-A	6.11 (± 0.14)*	688.26 (± 8.21)*
	UV-B	4.22 (± 0.22)*	835.45 (± 10.35)*
M-NP	PAR	10.30 (± 0.18)	474.26 (± 5.68)
	UV-A	6.35 (± 0.26)*	695.24 (± 14.21)*
	UV-B	4.38 (± 0.19)*	826.3 (± 13.35)*

The similar variation patterns of kinetic parameters for DOP uptake were observed in NM-NP and M-NP groups, when $V_{\max}$ further decreased after UV radiation (40.4%-60.2%) and increase of K_m was also enhanced comparing to that in NM-P group. In addition, $V_{\max}$ and K_m in UV-A and UV-B treatment did not differ significantly ($p > 0.05$) in NM-NP and M-NP groups, indicating a small effect of DOM in DOP-free medium.

3.5.2 Cellular P quota and P fractions in the medium

The fast accumulation and slow utilization of DOP *M. aeruginosa* was observed in DOP-rich medium, and results were distinct in NM-P and M-P groups (Fig. 5a and 5b). In NM-P group, cellular P quota was lower after UV radiation ($p < 0.05$) and DOP decline in the medium was slower, with more pronounced effects in UV-B treatment. Meanwhile, *M. aeruginosa* could produce more DIP in PAR treatment in NM-P group and

DIP content in the medium showed lower values after UV radiation. In M-P group, the promotion effect of UV radiation on cellular P quota was observed, which was also stronger in UV-B treatment. Consistently, DOP decline in the medium was faster after UV radiation but DIP showed high values in both three treatments in M-P group.

In the DOP-free medium, cellular P quota decreased gradually with *M. aeruginosa* growing in PAR treatment in NM-NP and M-NP groups. Meanwhile, cellular P quota also had a downward trend in UV-A and UV-B treatments, even though *M. aeruginosa* did not grow after UV radiation. Moreover, the detailed variation patterns also did not differ significantly ($p > 0.05$) in NM-NP and M-NP groups.

3.6. Effects on APase of *M. aeruginosa*

3.6.1 APA after irradiation treatments

Since the absorbance peak of *M. aeruginosa*-derived APase centered around 280–315 nm and the light absorbance was lower in PAR (Fig. S7), APA of algal cultures did not change obviously after 5 h of PAR, but it decreased obviously after UV-A (26.4%) or UV-B (40.0%) radiation in NM-P group (Fig. 5). During the 10-day recovery period, APA increased gradually and it showed the higher values in PAR treatment until Day 4. In M-P group, APA decreased slightly after UV radiation (8.8%-16.8%) and it increased quickly after withdrawing UV radiation, with similar variation patterns of APA in three treatments during the whole incubation.

In M-NP and NM-NP groups, APA of algal cultures both increased before Day 4 and decreased afterwards in PAR treatment. In NM-NP group, the inactivation of algal APA was more serious, which dropped by 32.8%-58.4% after UV radiation and leveled off after Day 4. In M-NP group, APA exhibited a greater decrease (42.4%-85.8%) after UV radiation and the inactivation of algal APA was also higher in UV-B treatment.

3.6.2 APA Inactivation under irradiation

As shown in Fig. 7, the irradiation treatments and DOM had significant interactive effects ($p < 0.05$) on the inactivation of *M. aeruginosa*-derived APase, with an apparent first-order decrease of APA. In the dark, APase had a good stability and its inactivation was enhanced ($p < 0.05$) with DOM addition. Under PAR, the high persistence of APase was also observed and the effect of DOM addition on APase inactivation was slowed down. Consistent with previous results, the evident inactivation of APase emerged after UV radiation. Meanwhile, the addition of DOM could significantly suppress ($p < 0.05$) the inactivation of APase in UV-A and UV-B treatments.

4. Discussion

4.1. Effects of DOP and DOM on algal UV adaptation capability

Our previous study has reported that exposure to ambient-intensity UV radiation had an inhibitory effect on the growth and photosynthesis of *M. aeruginosa*, but the influences could be eliminated with high DIP availability (Ren et al. 2020). The similar effects of UV radiation on *M. aeruginosa* emerged in DOP-rich waters, but the negative effects could be only eliminated with the addition of DOM.

The supply of DIP could directly affect the capability of phytoplankton to produce ATP as a substrate of phosphorylation and participate in other physiological processes (Heraud et al. 2005; Shelly et al. 2005). By comparison, DOP utilization by algae was usually an indirect process, when DOP was firstly associated with surface enzymes and then hydrolyzed to DIP by algae (Ren et al. 2017). In our study, the strong adaptation capability of *M. aeruginosa* to UV radiation was observed in M-P group, together with the less affected APA of algal cultures, enhanced utilization of DOP and high DIP in the medium during the incubation. This indicated that the adaptation of *M. aeruginosa* to UV radiation could be mainly achieved through the hydrolysis of DOP and metabolism of DIP for processes such as energy production, resynthesis of proteins, etc. (Litchman et al. 2002; Harrison et al. 2013). Hence, the decreased APA and weaker DOP utilization by *M. aeruginosa* after UV radiation in NM-P group resulted in low DIP content in the culture medium and evident negative effects on *M. aeruginosa*. There were also reports elsewhere about algal preferences to utilize different forms of nutrients when they were under environmental stresses (Ferber et al. 2004; Paerl et al. 2011). It was consistent with Korbee et al. (2012) that an increase in extracellular APA under UV radiation stress could constitute an additional mechanism that favored algal acclimation by augmenting inorganic P availability in the water. Consequently, the lowest UV adaptation capability of *M. aeruginosa* was observed in the DOP-free medium, when only traces of DIP was detected in the culture medium.

Studies have demonstrated that many environmental factors could greatly affect algal adaptation processes after UV-radiation (Yang et al. 2012; Helbling et al. 2011). For example, Li et al. (2017) reported that the iron-deficient cyanobacteria were more susceptible to UV-B radiation and the effects of UV radiation could be underestimated in natural waters. Carrillo et al. (2015) found that the mechanism of algal acclimation to UV radiation in the high-mountain lakes was related to the variations of algal internal P-content. This was also the case in our study that, DOM availability could change the photochemical reactions of APase and had an impact on DOP utilization property of *M. aeruginosa* in DOP-rich waters, leading to different UV adaptation capabilities. More specifically, DOM could protect algal APase from substantial inactivation and result in strong UV adaptation capability under UV radiation in the DOP-rich medium. The roles of DOM in water have been widely explored in recent years, including light attenuation, photochemical reaction, the release of nutrient, etc. (Schiebel et al. 2015; Hu et al. 2017). Although UV adsorption by DOM has been reported (Zhang et al. 2011), this was not main function of DOM in our study in consideration of the negligible effects of DOM on algal UV adaptation capability in DOP-free medium. Furthermore, since APase were mainly located on the outer surfaces of algae or as freely dissolved enzymes (Cao et al. 2009; Wang et al. 2014), UV radiation could easily reach algal APase before light was adsorbed by HA or UV-absorbing compounds (UVCs) in the 2-cm depth dishes (Ferroni et al. 2010; Espeland and Wetzel 2001).

4.2. Relation between algal UV adaptation and DOP utilization behavior

Scholars have shown that cyanobacteria have many effective strategies to alleviate the harmful effects of UV radiation, such as production of UVCs to mitigate the photo-induced damages, vertical migration of cells to decrease the irradiation stress, enhanced self-repair on short time scales (Hader et al. 2007; Helbling et al. 2011; Qin et al. 2015). Similarly, UV adaptation capability of *M. aeruginosa* in this study included decreasing UV-induced damages and increasing self-repair efficiency. Confirmed by the increase of intracellular ROS, the enhanced production of CAR and PC, and integrity of cells in SEM analysis in UV-A and UV-B treatments, UV radiation exerted oxidative stresses rather than direct lethal effects on *M. aeruginosa* in this study (Hessen et al. 2010; Ren et al. 2020). Since the up-regulation of CAR and PC could serve as the photoprotective compounds for cyanobacteria and enhance its light usage efficiency, and *M. aeruginosa* could increase SOD activity accordingly to scavenge ROS (Li et al. 2017; Zhang et al. 2013), *M. aeruginosa* resurrected its photosynthetic activity and continued to grow in varying degrees after withdrawing UV radiation in DOP-rich medium. In comparison, *M. aeruginosa* could not synthesize enough CAR and PC, and ROS was not efficiently scavenged in DOP-free medium, resulting in the poor UV adaptation capability.

It has been reported that UV radiation had a great impact on the nutrient utilization behaviors and cell-nutrient contents of phytoplankton, which might in turn significantly influence the adaptation of algae (Shelly et al. 2005; Carrillo et al. 2015). For example, Medina-Sánchez et al. (2006) reported that the deleterious effects of UV radiation on algae in the oligotrophic ecosystems were largely restricted by nutrient availability and depended more on cell nutritional status. In our experiment, DOP utilization behaviors of *M. aeruginosa* showed great changes during the UV adaptation processes, which had a close relationship with DOM availability in the culture medium.

As reported by previous studies (García-Gomez et al. 2012; Ren et al. 2020), UV adaptation processes of *M. aeruginosa* under sublethal UV radiation could result in an elevated P demand and they highly depended on cellular P content and DIP availability in the water. The acquired P could be used to activate expression of genes related to UV adaptation or to directly synthesize various metabolites for algal repair. Moreover, algae under UV exposure might depend more on the external DIP partly due to its inability to mobilize stored P (Shelly et al. 2005). However, inactivation of APase of *M. aeruginosa* cells after UV radiation in NM-P group could hinder algal ability to produce DIP for its utilization, when the negative effects included algal worse affinity to DOP, slower DOP uptake rate and lower cellular P quota. This was in accordance with Tank et al. (2005) and Sereda et al. (2011) that, the disrupted P cycling and reduced P acquisition ability of planktons after UV radiation could be partly caused by APA declines. Consequently, the P demand of cells after UV radiation did not be sufficiently met in NM-P group and *M. aeruginosa* growth was inhibited. But with algal affinity to DOP unaffected after UV radiation in M-P group, P demand of *M. aeruginosa* was met with the faster DOP uptake rate, higher cellular P quota and higher DIP production. In this case, algal SOD activity increased in accordance with higher ROS production under UV

exposure, and the superior up-regulation of CAR and PC by *M. aeruginosa* was conducive to its self-repair, leading in the strong UV adaptation capability. Since *M. aeruginosa* could not eliminate UV-induced effects through above-mentioned adaptation processes or sustain its normal growth with stored P in DOP-free medium, F_v/F_m of UV-radiated algae did not recover to the initial value and the worst UV adaption capability was observed.

4.3. Roles of DOM on APase Inactivation

Although many studies have examined the kinetic and fate of APase under varying conditions (Ren et al. 2015; Ma et al. 2019); limited information was provided on the effects and regulation of irradiation and DOM, despite the complex light conditions and widespread presence of DOM in natural waters.

It was reported that APase was stable in water and could remain active for several days, but HA occupying the main part of DOM pool could directly associate with APase (Boavida et al. 1998; Sun et al. 2014). Our study supported previous data and HA might block the active sites of APase, leading to APA decrease in the dark. However, effects of DOM on APase inactivation decreased in the PAR treatment, when PAR might break down the binding between HA and APase (Scully et al. 2003). Consequently, APA of the cultures of *M. aeruginosa* did not decrease after 5-h of PAR in both four groups, and DOP cycling by algae might not be significantly affected.

In comparison, UV radiation caused oxidative stresses on *M. aeruginosa* by ROS, which resulted in the inactivation of APase in UV-A and UV-B treatments (Janssen et al. 2014). Moreover, the absorbance of UV-band light by APase was high (Fig. S2) and the direct oxidation of APase might occur after UV radiation (Janssen et al. 2015). But suitable electron donors could convert radical cations of amino acids back to the ground states (Galano et al. 2010; Shen et al. 2018), and DOM likely played as antioxidant to repair the oxidized APase, resulting in the slower inactivation of APase and slight APA decrease of algal cultures. The antioxidant potential of HA was also detected in some other laboratory experiments (Dhanapal and Sekar 2014; Ozfidan-Konakcia et al. 2018). Another less-specific mechanism that underlies APase inactivation in M-P group was the complexation of DOM with APase while retaining high activities, thus displaying a stabilization effect on APase (Espeland and Wetzel 2001). The higher APA decrease in algal cultures in M-NP group could be that, composition of extracellular organic matter (EOM) of *M. aeruginosa* was complicated (Xu et al. 2013), which could also act as a photosensitizer to generate more ROS in the water (Janssen et al. 2015).

In many aquatic systems, DIP shortage has become a common phenomenon and DOP released from sediments and external DOP inputs are becoming the major sources of P loading (Bai et al., 2009; Ren et al. 2017). Considering the wide distribution of *M. aeruginosa* in eutrophic lakes, our results could partly provide a framework to elucidate the mechanisms that enable cyanobacteria to utilize DOP and adapt UV radiation in the natural waters. However, the complexities and unexamined factors deserve a further study in the future.

5. Conclusions

- (1) Short-term ambient UV-A and UV-B radiation exerted oxidative stresses on *M. aeruginosa* and exhibited inhibitive effects on the growth and photosynthesis of algae in the DOP-rich waters. The negative effects of UV radiation could be eliminated with DOM addition (5 mg L^{-1} of HA), when *M. aeruginosa* showed a strong UV adaptation capability. Meanwhile, *M. aeruginosa* had the lowest UV adaptation capability in the DOP-free medium and no significant effects of DOM addition were observed.
- (2) The adaptation of *M. aeruginosa* to UV radiation in DOP-rich waters could be mainly achieved through the hydrolysis of DOP and metabolism of DIP, which included decreasing UV-induced damages and promoting self-repair. DOM addition in the DOP-rich medium could enhance DIP production by *M. aeruginosa* after UV radiation, and increase the production of CAR, PC, and SOD activity of algal cells.
- (3) APase inactivation after UV radiation caused the worse affinity to DOP, slower DOP uptake rate and lower cellular P quota of *M. aeruginosa*, when algal P demand for UV adaptation could be not met in this case. However, DOM could act as an antioxidant and decreased APase inactivation under ambient UV radiation, and DOP utilization by *M. aeruginosa* was promoted for UV adaptation.

6. Abbreviations

NM-P group [without DOM in DOP-rich medium]; M-P group [with DOM in DOP-rich medium], NM-NP group [without DOM in DOP-free medium], M-NP group [with DOM in DOP-free medium]; DOP [dissolved organic phosphorus]; DIP [dissolved inorganic phosphorus]; DOM [dissolved organic matter]; APA [alkaline phosphatase activity]; SOD [superoxide dismutase]

7. Declarations

Ethics approval and consent to participate: Not applicable

Consent for publication: Not applicable

Availability of data and materials: The datasets used and analyzed during the current study are available from the corresponding author on reasonable request.

Competing interests: The authors declare that they have no competing interests.

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Figures

Figure 1

Effects of different irradiation on the growth of *M. aeruginosa* in (a) high-DIP medium, (b) moderate-DIP medium, (c) NM-P group, (d) M-P group, (e) NM-NP group, and (f) M-NP group

Figure 2

Photosynthetic efficiency of *M. aeruginosa* after 5-h of irradiation and during 10-day recovery period in (a) NM-P group, (b) M-P group, (c) NM-NP group, and (d) M-NP group. (Arrow indicates the initial value of F_v/F_m and dash lines indicate the differences of its decline after UV radiation; * indicates a significant difference between UV-A or UV-B treatment and PAR control at $p < 0.05$)

Figure 3

Changes of (a) algal antioxidant responses, (a) chlorophyll-a, (c) carotenoids, and (d) phycocyanin contents in single cells after 5-h of different irradiation (Arrows indicate the initial values of photosynthetic pigment)

Figure 4

SEM images of *M. aeruginosa* cells on Day 1 in NM-P, M-P, NM-NP and M-NP groups after 5-h of different irradiation

Figure 5

Cellular P quota of *M. aeruginosa* (vertical bar) and the contents of P fractions in the medium (line and scatter, solid line referred to DOP and dashed line referred to DIP) in (a) NM-P group, (b) M-P group, (c) NM-NP group, and (d) M-NP group after different irradiation treatment

Figure 6

APA of algal cultures in (a) NM-P group, (b) M-P group, (c) NM-NP group, and (d) M-NP group after different irradiation treatment

Figure 7

Effects of irradiation and DOM on the inactivation of *M. aeruginosa*-derived APase: (a) dark, (b) PAR, (c) UV-A radiation, and (d) UV-B radiation

Supplementary Files

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