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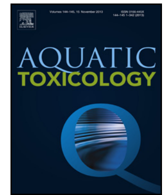

Research paper

Different physiological and photosynthetic responses of three cyanobacterial strains to light and zinc

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ABSTRACT

Zinc pollution of freshwater aquatic ecosystems is a problem in many countries, although its specific effects on phytoplankton may be influenced by other environmental factors. Light intensity varies continuously under natural conditions depending on the cloud cover and the season, and the response mechanisms of cyanobacteria to high zinc stress under different light conditions are not yet well understood. We investigated the effects of high zinc concentrations on three cyanobacterial strains (*Microcystis aeruginosa* CPCC299, *M. aeruginosa* CPCC632, and *Synechocystis* sp. FACHB898) grown under two light regimes. Under high light condition (HL), the three cyanobacterial strains increased their Car/Chl *a* ratios and non-photochemical quenching (NPQ), with CPCC299 showing the highest growth rate—suggesting a greater ability to adapt to those conditions as compared to the other two strains. Under high zinc concentrations the values of maximal (Φ_M) and operational (Φ'_M) photosystem II quantum yields, photosystem I quantum yield [*Y*(I)], and NPQ decreased. The following order of sensitivity to high zinc was established for the three strains studied: CPCC299 > CPCC632 > FACHB898. These different sensitivities can be partly explained by the higher internal zinc content observed in CPCC299 as compared to the other two strains. HL increased cellular zinc content and therefore increased zinc toxicity in both *M. aeruginosa* strains, although to a greater extent in CPCC299 than in CPCC632. Car/Chl *a* ratios decreased with high zinc concentrations under HL only in CPCC299, but not under low light (LL) conditions for all the studied strains, suggesting that the three strains have different response mechanisms to high zinc stress when grown under different light regimes. We demonstrated that interactions between light intensity and zinc need to be considered when studying the bloom dynamics of cyanobacteria in freshwater ecosystems.

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1. Introduction

Cyanobacteria are widely distributed in freshwater and seawater ecosystems, and some species form blooms that decrease water quality and provoke negative impacts on phytoplankton, zooplankton, and animals (Carmichael, 2001; Codd, 1995; Metcalf and Codd, 2009; Paerl and Otten, 2013). Cyanobacterial blooms are formed by fast growing species found at the surfaces of waterbodies, and they are influenced by various environmental factors including light, temperature, nutrient concentrations, and pollutants (Peters et al., 2013; Watanabe and Oishi, 1985; Xu et al., 2012; Yamamoto and Nakahara, 2005).

Zinc is a micronutrient necessary for photosynthesis and cyanobacterial growth at low concentration (<1 μM), although it becomes toxic when its concentration reaches a threshold level (from micro- or millimolar). Zinc concentrations in polluted aquatic ecosystems may range from 61 μg/l (1 μM, Taihu lake, China) (Su et al., 2012) to 2967 μg/l (46 μM, Earthen pond close to Cross River State, Nigeria) (Ada et al., 2012). High zinc concentrations in lakes and rivers may therefore affect the physiological processes of phytoplankton, species distributions, and cyanobacterial bloom formation (Bbosa and Oyoo, 2013; Chaloub et al., 2005; De Magalhães et al., 2004). Various studies have been undertaken to better understand the physiological responses of cyanobacteria to zinc stress, and high concentrations of this metal have been found to provoke decreases in pigment contents (chlorophyll *a*, carotenoids, and phycobilisomes) and in photosystem II (PSII) activity, and to inhibit energy transfer from phycobilisomes to PSII centers—with the consequent inhibition of photosynthesis and growth (Okmen et al., 2011; Xu et al., 2013; Zeng et al., 2009). Different cyanobacterial species show different sensitivities to high zinc concentrations (Okmen et al., 2011), as *Nostoc punc-*

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tiforme, for example, can tolerate zinc concentration of 1430 μg/l that is toxic to most cyanobacteria (Hudek et al., 2012). Differences in zinc tolerance have been observed even within the same genus, with *Spirulina indica*, *Spirulina maxima,* and *Spirulina platensis*, for example, showing different sensitivities to high concentrations of that metal (Balaji et al., 2014).

Zinc toxicity is not only species-dependent, but can also be influenced by the co-occurrence of other environmental factors such as light (Chaloub et al., 2005; Zeng and Wang, 2011). Since changes in light intensity affect photosynthesis and cyanobacterial growth, light availability will alter cyanobacterial distribution in freshwater ecosystems (Ibelings et al., 1994). Light has also been shown to affect metal uptake and toxicity in phytoplankton (Xu et al., 2013; Zeng and Wang, 2011), although most studies assessing zinc toxicity in cyanobacteria have focused solely on the effects of different zinc concentrations (without considering other environmental factors) or its effects on just a single physiological process (such as zinc uptake efficiency or PSII–PSI electron transport rate). As such, the abilities of different cyanobacteria to cope with high zinc concentrations under different environmental conditions (such as light intensity) have been only incompletely examined.

We investigated here the photosynthetic and physiological responses of three cyanobacterial strains to short term high-zinc stress under two different light intensities, and found that zinc uptake rates were different among them, leading to different sensitivities and varying responses to high zinc exposure.

2. Materials and methods

2.1. Cultures

Microcystis aeruginosa CPCC299 (hereafter referred to as CPCC299) and *M. aeruginosa* CPCC632 (hereafter CPCC632) were obtained from the Canadian Phycological Culture Centre. *Synechocystis* sp. FACHB898 (hereafter FACHB898) was obtained from the Freshwater Algal Culture Collection of the Institute of Hydrobiology, Chinese Academy of Sciences. CPCC299 is a toxic cyanobacterial strain and produces microcystins at concentrations of up to 38 fg/cell (Xu et al., 2013), whereas CPCC632 and FACHB898 are non-toxic strains. The three strains were cultured at 22 °C in 250 ml flasks containing 120 ml of modified bold basal media (BBM) at pH 6.8 (Stein, 1973). The BBM was modified by decreasing the micronutrient content (except zinc) to 10% of the original formula, for controlling the metal species in the solution (Twiss et al., 2001). The zinc concentration in the modified BBM was 0.78 μM (pZn 8.9). In order to avoid external zinc contamination, all the glassware used was soaked with 10% HCl overnight and thoroughly rinsed (at least three times) with Milli-Q water (18.2 MΩ) before use. The cultures were grown under a 14:10 h light:dark cycle at either 50 μmol photons m^{-2} s^{-1} illumination (LL) or 300 μmol photons m^{-2} s^{-1} illumination (HL) provided by a combination of incandescent and white fluorescent sources (Philips F72T8/TL841/HO, USA). The three strains were cultured for at least eight generations (two months) under either of the two light conditions, with sub-samples being taken every day for cell density measurements using a Multisizer™ 3 Coulter Counter® (Beckman Coulter Inc., Brea, CA, USA). The specific growth rates were calculated from cultures in their exponential phase: $\mu = (\ln(N_6) - \ln(N_2))/4$; where N_6 is the cell concentration on day six, and N_2 is the cell concentration on day two.

2.2. High zinc treatment

Cultures in their exponential phase were harvested by gentle filtration onto 0.8 μm filters (Xingya Purifying Materials Factory, Shanghai, China) and re-suspended in fresh modified BBM at three different zinc concentrations. Cell concentrations were maintained at 3.5×10^5 cells/ml for all experiments. The cyanobacteria were exposed to three different zinc concentrations (0.78 μM [pZn 8.9] as the control, and 7.8 μM [pZn 5.6] and 39 μM [pZn 4.8)] as the two high-zinc concentrations) for 4.5 h under the two illumination conditions, after which they were moved to dark condition for 30 min before further measurements. We chose these high-zinc concentrations since they can be found in natural freshwater (Bbosa and Oyoo, 2013; Su et al., 2012; Ada et al., 2012). Free zinc concentrations were calculated using Visual MINTEQ Version 3.0 (Gustafsson JP, http://www.lwr.kth.se/english/OurSoftware/vminteq/). The true zinc concentrations in the medium were confirmed by atomic absorption spectrometry (see Section 2.5).

2.3. Pigment measurements

The pigment profiles of the three cyanobacterial strains were measured spectrophotometrically. Culture cell densities were determined using 1 ml sub-samples, as described above. The samples were then harvested by filtration, re-suspended in methanol, boiled for 5 min, and the extracts subsequently stored overnight at −80 °C. After filtration through a GFF filter (Whatman, Piscataway, NJ, USA), the absorbance spectra of the extracts were measured using a Cary 300 UV–vis spectrophotometer (Varian Australia Pty., Ltd., Mulgrave, VIC, Australia). The chlorophyll *a* (Chl *a*) and carotenoid (Car) contents were calculated according to Ritchie (2008), based on their absorbances at 470 nm, 632 nm, 652 nm, 665 nm, and 696 nm.

2.4. PSII activity and non-photochemical quenching determinations

After 30 min of dark acclimation, cyanobacteria sub-samples were taken to measure PSII activity using a WATER-PAM Chlorophyll Fluorometer (Walz GmbH, Effeltrich, Germany). The minimal fluorescence yield (F_0) was determined in the absence of actinic illumination. The actinic light was then turned on (at the same intensity as the growth culture intensity) for 1 min, and the fluorescence yields F' and F_M' were determined briefly before or during a saturating light pulse (800 ms, 3000 μmol photons m^{-2} s^{-1}) respectively. The actinic light was then turned off and DCMU was added to the sample and the maximal fluorescence yield in the presence of DCMU (F_M) was determined. Maximal PSII quantum yields with DCMU (Φ_M) and with light (Φ'_M), and non-photochemical quenching (NPQ) were calculated using the following equations: $\Phi_M = (F_M - F_0)/F_M$ (Kitajima and Butler, 1975); $\Phi'_M = (F_M' - F')/F_M'$ (Genty et al., 1989), and $NPQ = (F_M - F_M')/F_M'$ (Bilger and Björkman, 1990).

2.5. PSI activity measurements

PSI transmittance was measured by using a dual-wavelength pulse-amplitude-modulated fluorescence monitoring system (Dual-PAM, Heinz Walz, Effeltrich, Germany), following Perreault et al. (2009). The modulated, actinic, and saturating pulse (800 ms) light intensities used were 1 μmol photons m^{-2} s^{-1}, 53 or 300 μmol photons m^{-2} s^{-1} and 3000 μmol photons m^{-2} s^{-1} respectively. The PSI quantum yield was calculated according to Klughammer and Schreiber (2008): $Y(I) = (P_M' - P)/(P_M - P_O)$.

2.6. Intracellular zinc concentration measurements

After 4.5 h of exposure to light and a 0.5 h dark acclimation (hereafter 5 h exposure) the samples were filtered and washed with 10 ml of 0.1 mM EDTA for 3 min to remove any loosely adsorbed

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