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Interactive effects of temperature and copper toxicity on photosynthetic efficiency and metabolic plasticity in *Scenedesmus quadricauda* (Chlorophyceae)

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Abstract
Warming and copper (Cu) toxicity are two key abiotic stressors that strongly affect cell growth, photosynthetic rate, and metabolism in microalgae. In this study, a freshwater chlorophyte, *Scenedesmus quadricauda*, was exposed to various concentrations of copper sulfate (300, 600, and 1000 μM nominal concentrations of $CuSO_4 \cdot 5H_2O$) at 25 and 35 °C. The changes in cell density, photosynthetic parameters, in vivo absorption spectra, reactive oxygen species (ROS) levels, and metabolic profile were analyzed. The effects of copper toxicity on the physiology and biochemistry of microalgae were highly dependent on water temperature. The interactive effects of both stressors induced significant impact on the photosynthetic parameters such as maximum quantum yield (F_v/F_m), saturation irradiance (E_k), and non-photochemical quenching (NPQ). Temperature induced significant impact on cell density, E_k and NPQ, while the Cu toxicity significantly affected the F_v/F_m and NPQ. Changes in the in vivo absorption spectra and high levels of reactive oxygen species (ROS) were observed across different treatments. Overall, *S. quadricauda* adapted to the two abiotic stresses via NPQ and metabolic restructuring. Key metabolites including glycine, proline, hexadecanoic acid, propanoic acid, octadecanoic acid, galactose, lactose, and sucrose were involved in the microalgal response. The synergistic effects of temperature and Cu stresses on microalgae might affect community tolerance and species distribution in the long run.

Keywords Temperature stress · Copper toxicity · Chlorophyceae · *Scenedesmus* · Photosynthesis · Metabolomics

Introduction

Over the last decades, copper (Cu) contamination in aquatic ecosystems due to anthropogenic activities has become a major concern (Harvey et al. 2016; Chen et al. 2017; Khodami et al. 2017). In photosynthetic organisms, Cu is an essential trace metal involved in the electron transfer, redox reaction, signaling mechanisms, and oxidative stress response of microalgae (Castruita et al. 2011; Kropat et al. 2015). However, when present at high concentrations, Cu is known to induce toxic effects on microalgae by affecting chlorophyll synthesis, photosynthetic efficiency, growth, reactive oxygen species (ROS) generation, and gene expression (Suresh Kumar et al. 2014; Adrees et al. 2015).

Microalgal sensitivity to copper is dependent on other ecological factors such as temperature, pH, and salinity (Suresh Kumar et al. 2015). Among the different ecological conditions, global warming and aquatic toxicology have been closely associated with microalgal metabolism, species abundance, and diversity (Winder and Sommer 2012). Global warming is one of the contributing factors to the decline of annual global phytoplankton biomass over the past century (Boyce et al. 2010). Elevated temperature altered photosynthetic performance and regulated metabolic network of microalgae (Fanesi et al. 2016; Lee et al. 2017; Barati et al. 2018).

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