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Review

Macrophytes-cyanobacteria allelopathic interactions and their implications for water resources management—A review

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ABSTRACT

Macrophytes and phytoplankton including cyanobacteria are main primary producers in aquatic environments.Macrophytes can maintain water quality by suppressing phytoplankton growth through a number of mechanisms: while e.g. the absorption of high amounts of nutrients and the provision of refuge from predation for herbivorous aquatic fauna are widely accepted macrophyte functions, the role of their release of allelopathic substances in suppressing phytoplankton is increasingly being studied. Some macrophyte species can support the growth of epiphytic cyanobacteria providing them an advantage over planktonic species in the competition for nutrients. On the other hand, some cyanobacteria dominate in eutrophic water bodies and produce cyanotoxins that exert allelopathic substances which may contribute to the decline of macrophytes. Macrophytes can interact with these cyanotoxins in different ways including bioaccumulation and biotransformation. This review focuses on such allelopathic interactions between macrophytes and toxic cyanobacteria. The article also suggests methods for researchers and water resources managers for the application of macrophytes to control harmful cyanobacterial blooms and as phytoremediators for toxin elimination from water bodies.

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1. Introduction

Macrophytes and phytoplankton are main primary producers in aquatic environments. Macrophytes influene nutrient cycling by transferring them from sediment to water where they can be used by phytoplankton and bacteria (Camargo et al., 2003). Macrophytes may affect nutrient cycling by retention of nutrients in their submersed roots and leaves, restricting nutrient availability to phytoplankton (Pott and Pott, 2003). They also provide refuge for macro invertebrates, zooplankton and young fish (Mulderij et al., 2007). Additionally, macrophyte metabolism may change some physicochemical properties of the water such as oxygen, inorganic carbon, pH and alkalinity (Caraco and Cole, 2002).

In general, shallow lakes may be clear with abundant macrophytes or turbid with abundant phytoplankton (Scheffer et al.,

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2003), and may shift from one state to another. This shift is mainly due to eutrophication (i.e.high nutrient concentrations, particularly nitrogen and phosphorus) which tends to cause the turbid state with high phytoplankton density (Seto et al., 2013). However, the mutual inhibitory allelopathic activities of macrophytes and phytoplankton may also lead to the dominance of either macrophytes or phytoplankton (Scheffer, 1998). Many studies have shown that macrophytes can inhibit the growth of phytoplankton through releasing allelochemicals into aquatic environments (e.g. Nakai et al., 2012). On the other hand, phytoplankton, particularly cyanobacteria, can also produce wide range of bioactive compounds including toxins (Carmichael, 2001), and some of these in turn are proposed to exert different allelopathic effects on aquatic plants such as reduction in growth and changes in pigment composition, antioxidant enzymes and photosynthesis (Pflugmacher, 2002). As a result, some macrophytes have disappeared from eutrophic water bodies, while cyanobacterial blooms proliferate (Li et al., 2009). Furthermore, cyanotoxins can be realesd with high concentrations into drinking water if they are not properly treated at water treatment plants (Mohamed et al., 2015, 2016; Mohamed, 2016). Thereby, they deteriorate drinking water quality and pose a risk to human health upon consumption of toxin-contaminated water. In this review, we discuss the inhibitory and stimulatory alleoptahic activities of macrophytes on cyanobacteria in aquatic ecosystems. Also, we focus on the effects of cyanotoxins on the growth and metabolic processes of macrophytes and the potential interaction of macrophyte species with these toxins. Finally, we shed light on the role of macrophytes for the management of freshwater sources management to control harmful cyanobacterial blooms and remove cyanotoxins.

2. Allelopathic activities of macrophytes on cyanobacteria

Several studies have shown that macrophytes can successfully suppress phytoplankton growth by certain mechanisms including the reduction of light and nutrients or through the excretion of allelopathic substances. Competition for nutrients is generally less important, as most aquatic macrophytes are rooted and obtain most macronutrients from the sediments that usually contain high nutrient concentrations (Seto et al., 2013). Production and excretion of allelochemicals by aquatic macrophytes could be more effective against phytoplankton compared to light and nutrients (Donk and van de Bund, 2002). Macrophyte allelochemicals belong to different chemical classes such as polyphenols, oxygenated fatty acids, sulfur compounds, polyacetylenes (Nakai et al., 2012). Both field and laboratory studies have shown many macrophytes to have allelopathic effects on the growth and physiological processes of cyanobacteria (Table 1).The allelopathic activity of macrophytes depends on the chemical nature of allelochemicals as well as their production and excretion rate (Mulderij et al., 2007). The activity is also dependent on the specific toxicological mechanism of each allelochemical (Wang et al., 2013) and on the target cyanobacterial species as well (Mohamed and Al-Shehri, 2010).The phytoplankton group most sensitive to macrophyte allelochemicals is cyanobacteria followed by diatoms, whereas green algae are known to be less sensitive (Hilt and Gross, 2008). Allelopathic activities of macrophytes against phytoplankton and cyanobacteria were reported for at least 40 macrophyte species (Table 1). However, it seems that the most frequent submerged macrophytes in shallow lakes such as *Myriophyllum, Ceratophyllum, Elodea, Najas and Stratiotes* or certain charophytes are the most allelopathically active species. The allelochemiclas produced by these macrophytes act as growth inhibitor of bloom-forming toxic cyanobacteria (Liu et al., 2007; Shao et al., 2009).

2.1. Inhibitory allelopathic effects of macrophytes on cyanobacteria

Some macrophyte allelochemicals significantly inhibit the photosynthesis in several species of phytoplankton including cyanobacteria. For instance, the allelochemical tellimagrandin II produced by the macrophyte *Myrophyllum spicatum* was found to inhibit photosystem II (PSII) of *Anabaena* sp. through interfering with the electron transfer (Leu et al., 2002). Zhu et al. (2010) also demonstrated that the poyphenols pyrogallic acid and gallic acid produced by *Myriophyllum spicatum* decreased the photosynthetic activity of *M. aeruginosa* by inhibiting the activity of PSII. The PSII damage could be repaired by D1 protein, key subunit of photosystem II (Komenda and Masojidek, 1998). Nevertheless, other allelochemiclas such as pyrogallic acid could inhibit the expression of psbA gene encoding the D1 protein in *Microcystis* and *Cylindrospermopsis*, and thus prevent the synthesis of such a stress-adapting protein (Wu et al., 2013a). Some allelochemicals, e.g. polyphenols, strongly inhibit photosynthesis and electron transport activities of cyanobacteria rather than green algae, due to the different photosynthetic apparatuses in cyanobacteria and green algae (Zhu et al., 2010).The extracts, exudates and live material of *Chara australis* also exhibited strong inhibitory effects on the cyanobacterium *Anabaena variabilis*, but no effect was evident on the growth of the green alga *Scenedesmus quadricauda* (Pakdel et al., 2013). This finding indicates the selective inhibition of macrophyte allelochemicals towards the undesired cyanobacteria.This could be useful for biocontrol of algal blooms in aquacultures to remove harmful cyanobacteria and leave green algae to be used as food for fish. Moreover, the allelopathic effect of a macrophyte assemblage exudate (*Chara hispida, C. baltica, C. vulgaris, N. hyalina* and *Myriophyllum spicatum* in a mixed culture) resulted in stronger allelopathic effects against cyanobacteria and diatoms than monocultured macrophytes (Rojo et al., 2013a).The authors attributed this to the fact that these assemblages of macrophytes produced different allelopathic phenolic compounds as compared to the single species alone, which in turn, had synergistic effects by directly reducing microalgal biomass and by indirectly enhancing grazing, consequently promoting the occurrence of a clear-water phase. This finding suggests replanting with mixtures of submerged native macrophytes for restoration of aquatic ecosystems.

Based on many studies, oxidative damage has been considered as one of the important allelopathic and toxicological mechanisms of macrophyte allelochemicals acting against phytoplankton and cyanobacteria (Wu et al., 2007; Shao et al., 2009). Moreover, the reduction in algal photosynthesis may also be mediated by oxidative stress (Laue et al., 2014). This is due to the generation of excess O_2^- which triggers a free radical chain reaction and induces lipid peroxidation of cell membranes, changing their penetrability and leading to the eventual death of cyanobacterial cells, when superoxide levels exceed a breaking point (Zhang et al., 2011). Several allelochemicals have been reported to induce the cellular responses of antioxidant enzymes and non-enzymatic antioxidants. The allelochemical ethyl 2-methyl acetoacetate (EMA) produced by *Phragmites communis* was found to impose a marked oxidative stress with ultimate inactivation of antioxidant defense system of *M. aeruginosa* (Hong et al., 2008).The indole alkaloid gramine (*N,N*-dimethyl-3-aminomethylindole) produced by a giant reed (*Arundo donax*) affected both enzymatic and non-enzymatic antioxidants of *M. aeruginosa*, which were reduced sharply after 60 h of exposure (Hong et al., 2009). Zhang et al. (2010) demonstrated that two phenol acids, ρ-coumaric acid and vanillic acid, produced by *Vallisneria spiralis* increased $O_2^{\bullet -}$ and manodialdehyde (MDA) contents in *M. aeruginosa* cells. Wang et al. (2011) also provided a direct evidence of oxidative stress and ROS generation in cyanobacteria and green algae upon exposure to the allelochemicals catechin