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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.

Contents

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

Table 1
Allelopathic activity of aquatic plants and their allelochemicals against cyanobacteria.

Macrophyte	Type of plant material tested	Concentrations	Allelochemicals contained	Cyanobacteria inhibited	References
Emergent macrophytes					
Acorus calamus	Extract	0.05-0.1 mg FW ml^{-1}	Phenylpropanes	*Anabaena flos-aquae, Aphanizomenon flos-aquae, Microcystis aeruginosa*	Greca et al. (1989), Zhang et al. (2015)
Acorus gramineus	Extract	25 mg FW ml^{-1}	Phenylpropanes	*Microcystis aeruginosa*	Greca et al. (1989), Nakai et al. (2010)
Acorus tatarinowii	Exudate	50 g FW L^{-1}	Phenylpropanes	*Anabaena flos-aquae, Synecococcus leopoliensis*	Greca et al. (1989), He and Wang, (2001)
Arundo donax	Extract	0.5 mg DW ml^{-1}	Gramine (N,N-dimethyl-3-amino-methylindole)	*Microcystis aeruginosa*	Hong et al. (2009, 2010)
Eleocharis acicularis	Co-cultivation	2–3 g FW L^{-1}	Unknown	*Anabaena flos-aquae, Microcystis aeruginosa, Phormidium tenue*	Nakai et al. (1999)
Phragmites australis	Extract	9.4 mg FW ml^{-1}	Unknown	*Microcystis aeruginosa*	Nakai et al. (2010)
Phragmites communis	Extract fraction	0.79 mg DW L^{-1}	Ethyl 2-methylacetoacetate, phenolic acids (*p*-coumaric acid, ferulic acid), caffeic acid (gallic acid), fatty acid (stearic acid)	*Microcystis aeruginosa, Phormidium* sp.	Li and Hu, (2005), Zhou et al. (2006)
Scirpus tabernaemontani	Extract	100 mg FW ml^{-1}	Unknown	*Microcystis aeruginosa*	Nakai et al. (2010)
Thalia dealbata	Extract	0.1–1 mg DW ml^{-1}	Unknown	*Anabaena flos-aquae, Microcystis aeruginosa*	Zhang et al. (2011)
Typha latifolia,	Extract	8.5–17.1 mg DW ml^{-1}	Steroids, fatty acids.	*Anabaena flos-aquae, Microcystis aeruginosa,*	Aliotta et al. (1990),
Typha angustifolia	Extract	100 mg DW ml^{-1}	Phenic acids (o-hydroxycinnamic acid, syringic acid and isoferulic acid	*Synechococcus leopoliensis*	Zhang et al. (2012a)
Floating macrophytes					
Brasenia schreberi	Extract	0.1-0.5 mg DW ml^{-1}	Unknown	*Anabaena flos-aquae*	Elakovich and Wooten (1998)
Cabomba caroliniana	Co-cultivation	7–8 g FW L^{-1}	Unknown	*Anabaena flos-aquae, Microcystis aeruginosa, Phormidium tenue*	Nakai et al. (1999)
Eichhornia crassipes	Extract	1–2 mg DW ml^{-1}	N-phenyl-1-naphthylamine, N-phenyl-2-naphthylamine, linoleic acid, benzoindenone	*Anabaena azollae, Microcystis aeruginosa*	Wu et al. (2012)
Lemma minor	Co-cultivation	12 plant 0.5 L^{-1}	Unknown	*Microcystis aeruginosa*	Jang et al. (2007)
Nelumbo nucifera	Extract	25 mg FW ml^{-1}	Propanamide	*Microcystis aeruginosa*	Hu and Hong (2008), He et al. (2013)
.Pistia stratiotes	Extract.	0.06-0.1 mg DW ml^{-1}	Polyphenols, linoleic acid, linolenic acid, fatty acids, steroidal ketones	*Microcystis aeruginosa*	Aliotta et al. (1991), Wu et al. (2013b)
Stratiotes aloides	Extract	0.5–100 mg DW ml^{-1}	Moderately lipophilic non- phenolic compounds	*Anabaena variabilis, M. aeruginosa, Synechococcus elongatus*	Mulderij et al. (2007), Mohamed and Al-Shehri, (2010)
Submerged macrophytes					
Ceratophyllum demersum	Extract	10 mg DW ml^{-1}	Element sulfides, labile sulfur compounds	Cyanobacteria	Gross et al. 2003, Hu and Hong (2008)
Egeria densa	Co-cultivation	3–7 g FW L^{-1}	Unknown	Cyanobacteria	Nakai et al. (1999)
Elodea Canadensis Elodea nuttallii	Extract/Exudate	100 mg DW ml^{-1}/100–200 mg FW ml^{-1}	Phenolic compounds	Epiphytic cyanobacteria	Erhard and Gross (2006)
Hydrilla verticillata	Exudate Extract	0.3–10 g FW L^{-1} 0.2–1 mg DW ml^{-1}	Penolic compound (vanillic acid, protocatechic acid, ferulic acid, caffeic acid)	*Microcystis aeruginosa*	Wang et al. (2006), Gao et al. (2011), Zhang et al. (2012b)
Limnophila sessiliflora	Co-cultivation	5–10 g FW L^{-1}	Unknown	Cyanobacteria	Nakai et al. (1999)
Myriophyllum brasiliense	Extract	2 mg DW ml^{-1}	Polyphenol-like alleochemicals	*Microcystis aeruginosa*	Saito et al. (1989)
Myriophyllum spicatum	Co-cultivation	2.5–10 g FW L^{-1}	Tellimagrandin II, pyrogallic acid, gallic acid, ellagic acid, (+)-catechin	*Microcystis aeruginosa*	Nakai et al. (2005), Zhu et al. (2010)
Myriophyllum verticillatum	Extract	0.5–2 mg ml^{-1}	a-asarone, phenylpropane, glycoside-like allelochemicals	*Microcystis aeruginosa, Limnothrix redeke*	Aliotta et al. (1992), Hilt et al. (2006)
Najas marina	Extract	10 mg DW ml^{-1}	Hydrophilic and moderately lipophilic allelochemicals	*Anabaena variabilis, Synechococcus elongatus*	Gross et al. (2003)
Potamogeton malaianus Potamogeton maackianus Potamogeton pectinatusm	Co-cultivation/Exudate	5 g FW L^{-1}	diterpenes, linolenic acid	*Microcystis aeruginosa*	Hu and Hong (2008), Zhang et al. (2009)
Potamogeton pusillus	Exudate	3.8- 32.3 g DW L^{-1}	Unknown	*Microcystis aeruginosa*	Takeda et al. (2011)
Potamogeton lucens	Extract	7–28 g FW L^{-1}	Unknown	*Anabaena variabilis*	Jasser (1995)
Potamogeton crispus Potamogeton oxyphyllus	Extract/Exudate Co-cultivation	7 mg DW ml^{-1}/10 g FW L^{-1} 2.5 g FW L^{-1}	Unknown Unknown	*Anabaena variabilis Microcystis aeruginosa*	Pakdel et al. (2013) Nakai et al. (1999)
Vallisneria denseserrulata Vallisneria spiralis	Co-cultivation	10 g FW L^{-1}	2-ethyl-3- methylmaldeimide, carotene derivatives	*Microcystis aeruginosa*	Xian et al. (2006), Gao et al. (2011)
Chara aspra, C. globularis, Nitellopsis obtuse, Nitella gracilis	Extract	200 mg DW ml^{-1}	4-methylthio-1,2-dithiolane and 5-hydroxy-1,2,3-trithiane.	*Anabaena cylindrica, A. torulosa, Anabaenopsis elenkinii, M. aeruginosa*	Berger and Schagerl (2004)
Chara australis	Extract/Exudate	7 mg DW ml^{-1}/10 g FW L^{-1}	Unknown	*Anabaena variabilis*	Pakdel et al. (2013)
Chara hispida, C. vulgaris, C.baltica, Nitella hyalina	Exudates	75–182 g FW L^{-1}	Unknown	*Pseudanabaena sp*	Rojo et al. (2013a)

DW = dry weight, FW = Fresh weight.

and pyrogallic acid excreted by *M. spicatum*. Besides antioxidant enzymes, many species of cyanobacteria produce alkaline phosphatase enzyme that enables them to overcome the deficiency of inorganic phosphate in the environment by obtaining it from organic phosphoric compounds (Vrba et al., 1993). The inhibition of cyanobacterial extracellular alkaline phosphatase is considered as one mode of action of macrophyte allelochemicals (Gross et al., 1996). For instance, hydrolysable polyphenols from *M. spicatum* inhibited the growth and phosphatase activity of various coccoid and filamentous cyanobacteria, and this inhibition was enhanced under phosphorus limitation conditions (Gross et al., 1996). Mohamed and Al-Shehri (2010) also demonstrated the inhibition of alkaline phosphates activity of planktonic cyanobacteria e.g. *Anabaena variabilis* by moderately lipophylic extracts of the submerged macrophyte *Stratiotes aloides*.

2.2. Interaction between macrophytes and their epiphytic cyanobacteria

Although most studies showed that the effects of macrophytes on phytoplankton are of inhibitory nature, some studies revealed the ineffectiveness or even stimulation of these organisms by some macrophyte extracts/exudates or allelochemicals. In this context, Hilt (2006) found no significant effect of *M. spicatum* and *M. verticillatum* on suspended cultures of the cyanobacteria *Phormidium tenue* and *Oscillatoria limosa*. However, *Elodea nuttallii* even stimulated the growth of the epiphytic cyanobacterium *Synechococcus elongatus* (Erhard and Gross, 2006). Similarly, Mohamed and Al-Shehri (2010) showed that the aqueous-methanol extract of *S. aloides* stimulated the growth and microcystin production in the epiphytic cyanobacterium *Merismopedia tenuissima* and had no effect on the epiphytic *Leptolyngbya boryana*.

The absence of inhibitory allelopathic effects of macrophytes on epiphytic cyanobacteria growing on their surfaces may be explained by the adaptation and natural resistance gained by epiphytes against allelochemicals of host macrophytes by co-evolution (Reigosa et al., 1999; Hilt, 2006). Given the short generation times of bacterial strains (Finlay, 2002), the development of resistant strains against macrophyte allelochemicals may occur over a timescale of weeks (Vanderstukken et al., 2014).Moreover, some epiphytic species co-occurring with the donor plant could even benefit from the production of allelochemicals by the plant (Hilt, 2006; Mohamed and Al-Shehri, 2010), as these substances may provide an advantage for epiphytic species in competition with phytoplankton for nutrients.This leads to the development of epiphytes dependent on macrophyte host species (Cattaneo et al., 1998). On the other hand, epiphytes can also affect macrophytes through various ways including reduction in the growth of macrophytes due to their shading, nutrient and carbon competition and allelopathy (Tóth, 2013). In addition to allelopathic interactions between macrophytes and epiphytes, macrophyte morphotypes (architecture, leaf shape. . ..etc) can also affect the density and distribution of their epiphytes (Comte and Cazaubon, 2002; Nõges et al., 2010). In this context, several studies have revealed a positive association between the abundance of epiphytes and the macrophyte complexity (Tessier et al., 2008; Hinojosa-Garro et al., 2010; Ferreiro et al., 2011, 2013).Finally, the grazing of epiphytes by macroinvertebrtaes may also influence the density of epiphytes on the macrophytes, particularly when the macrophyte surface is flat and easy to reach as are the leaves of *Potamogeton* (Jones et al., 2000; Comte and Cazaubon, 2002). Therefore, it is difficult to detect alleopathic effects of macrophytes against their epiphytes due to co-evolution and development of resistant strains. Hence, to study potential macrophyte-epiphyte allelopathic interation, It may be important to use strains isolated from epihphytic material which has been in contact with the host macrophyte for a prolonged period of time.

2.3. Factors affecting macrophyte allelopathic activity

The effect of some environmental factors has been described as a main problem when studying macrophyte allelopathic activities in the aquatic environment (Gross et al., 2007; Zhu et al., 2010). For example, phosphorus and nitrogen limitation was found to influence the production and release of allelochemicals by submerged macrophytes (Gross, 2003) and the response of the target organism as well (Reigosa et al., 1999). However, this effect may depend on the nutrient status of both donor and target species. For instance, while phosphorus limitation increased the production of polyphenols in the macrophyte *M. spicatum,* it enhanced inhibition of alkaline phosphatase in cyanobacteria (Gross et al., 1996). Low nitrogen concentrations in the environment also resulted in an increased tellimagrandin II content in *M. spicatum* (Gross, 2003). Light may cause chemical changes of released macrophyte allelochemicals due to oxidation, polymerization or cleavage (Gross et al., 2007). Additionally, Cronin and Lodge (2003) detected higher production of allelochemials by aquatic plants under increased light conditions. Choi et al. (2002) also showed that sun-exposed shoots of *M. spicatum* and *M. verticillatum*, particularly apical meristems, had higher concentrations of total phenolic compounds than shade-adapted plants. In contrast to polyphenols, *M. spicatum* produced high concentrations of tellimagrandin II under low light conditions (Gross, 2003).

Bacteria may also play a significant role in the degradation of macrophyte allelochemicals (Gross, 2003). Until now, little is known about the fate or persistence of allelochemicals in the environment (Cheng and Cheng, 2015). However, a few studies investigated the biodegradationon of polyphenolic allelocemicals produced by macrophytes. Müller et al. (2007) demonstrated a pronounced effect of polyphenol-degrading bacteria isolated from *M. spicatum* on the inhibitory allelopathic activity of the macrophyte exudates against phytoplankton. Bauer et al. (2009, 2010) isolated bacteria capable of degrading polyphenolic tannic acid (TA) produced by *M. verticillatum*. Furthermore, it has been found that photolytically and microbially degraded TA reduced cyanobacterial growth rates more than respective dark treatments (Bauer et al., 2012). This indicates that degradation by-products may be more harmful than the allelochemical itself, and thus can increase allelopathic growth inhibiting effects.

More research on the fate and persistence of macrophyte allelochemicals is needed to understand their role in the aquatic environment.

Herbivory can be another factor affecting the dominance of certain macrophytes with allelopathic activity. In this respect, it has been found that herbivory on *M. spicatum* apical meristems containing high allelochemical concentrations severely hampered the negative allelopathic impact on phytoplankton, as feeding of *Acentria ephemerella* removed the macrophyte apical tips (Gross et al., 2001; Choi et al., 2002).The production of allelochemicals by macrophytes may vary in different seasons. For instance, Hilt et al. (2006) found that the strongest activity of allelopathic inhibition against phytoplankton by *M. verticillatum* is found in August. The growth stage of macrophytes may also influence the allelopathic activity, as some studies reported that young, actively growing macrophytes exhbit a higher allelopathic activity than older ones (Mulderij et al., 2003). As macrophytes produce different allelochemicals, they may have synergistic effect on target cyanobacterial species. Zhu et al. (2010) found that three different mixtures with different proportions of four polyphenols identified in *M. spicatum*-cultured solution exhibited synergistic effect on *M. aeruginosa*, and their combined effects were related to the prop-

erties, proportion and number of allelochemicals released by the macrophyte. Furthermore, the presence of various phytoplankton species in the aquatic environment can influence the sensitivity of some species to allelochemicals (Gregor et al., 2008). For instance, coexistence of cyanobacteria with other phytoplankton groups in aquatic ecosystem made them more susceptible to allelochemicals than when tested in unialgal cultures (Zhu et al., 2010). Conversely, Chang et al. (2012) demonstrated that the presence of the green alga *Desmodesmus armatus* turned the inhibitory allelopathic activity of *M. verticillatum* on the cyanobacterium *M. aeruginosa* into growth stimulation. Therefore, the synergistic effects of different allelochemicals on cyanobacteria and interactions of cyanobacteria with other phytoplabkton species in response to these allelochemicals may be relevant in biocontrol of cyanobacteria by macrophyte alleochemicals.

Most studies on allelopathic interactions between aquatic macrophytes and cyanobacteria have been performed in the laboratory with extracts or exudates from aquatic macrophytes containing extraordinarily high concentrations of allelochemicals (Table 1). In contrast, the concentrations of allelochemicals reported from natural environments by submerged macrophytes are much lower than EC_{50} values of individual allelochemicals (Hilt et al., 2006; Zhu et al., 2010). For example, the concentrations of polyphenols released by *Myriophyllum spicatum* were 5.2–76.6 $\mu g\,L^{-1}$ at the plant density of 100 g fw L^{-1} cultivated for 3 days in laboratory, whereas the EC_{50} values of individual polyphenol ranged from 0.65 to 5.5 $mg\,L^{-1}$ for their impact on different strains of *Microcystis aeruginosa* (Nakai et al., 2000). Moreover at long-term exposures, the allelopathic activity of macrophytes against cyanobacteria might nonetheless occur *in situ* at low allelochemial concentrations (Wang et al., 2013). In this context, Vanderstukken et al. (2014) provided evidence that the alleopathic activity of *Elodea nuttallii* is strong enough to control phytoplankton in relatively large-scale systems and over a relatively prolonged time span (>50 days). Pakdel et al. (2013) also suggested that the inhibitory effect of *Potamogeton crispus* and *Chara australis* on phytoplankton growth may be very strong in the field when the macrophyte covers large areas and allelochemicals are continually released.

3. Effect of cyanotoxins on macrophytes

Cyanobacteria form harmful blooms due to the eutrophication of water bodies, and climate change may enhance this. Cyanobacteria produce a wide range of secondary metabolites that are very diverse in chemical structure and functions (Nunnery et al., 2010). Nevertheless, we limited our study to the selection of metabolites termed "cyanotoxins" due to their effect on vertrebrates merely because there is a fairly large number of publications addressing these; however, it is readily possible that other secondary metabolites (not necessarily with deleterious effects on vertebrates) will also prove to have effects – maybe even stronger ones – on macrophytes. Several species of cyanobacteria produce different cyanotoxins including hepatotoxins (e.g. microcystin, nodularin, cylindrospermopsin), neurotoxins (e.g. anatoxins, saxitoxins) and skin irritant toxins (Codd et al., 2005; Table 2). Cyanotoxins may occur both within the cells (cell-bound or intracellular) or dissolved in water (extracellular). While microcystins are rarely found dissolved in water and where blooms lyse and release larger amounts they degrade very quickly, the other cyanotoxins do show substantial fractions of dissolved toxin, and there is indication that cyanobacteria actively release cylindrospermopsin into the medium (Preußel et al., 2014). While Anatoxin-a is known to degrade very rapidly (Botana, 2007), there is indication of pronounced persistence of cylindrospermopsin (Wiedner et al., 2008). Cyanotoxins inhibit the growth and affect many metabolic processes of co-occurring biota including aquatic plants, resulting in a decline or even loss of most macrophyte species (Zheng et al., 2013).Consequently, the conditions in the lakes will shift towards turbid and phytoplankton dominance (Lombardo et al., 2013).

3.1. Effect of cyanotoxins on macrophyte growth, photosynthesis and antioxidant system

The different harmful effects that cyanotoxins exert on aquatic macrophytes include reduction in growth, chlorophyll contents, detoxication enzymes and photosynthetic capacity and changes in plant pigment composition (Pflugmacher, 2002; Table 2). Microcystins (MCs), the most common cyanotoxins, were found to exhibit inhibitory effects on the growth of several macrophyte species (Hu and Hong, 2008). MCs can also decrease the production of photosynthetic oxygen and change the pigment pattern and content in *C. demersum* and *Myriophyllum spicatum* (Pflugmacher, 2002; Jang et al., 2007) and *Vallisneria natans* (Jiang et al., 2011). Charophyte species were affected by MC exposure, and this effect was species-dependent: The presence of MC-LR largely reduced the growth rates, chlorophyll-a concentration and photosynthetic rates of *Chara hispida* and *C. aspera*, whereas those of *C. vulgaris, C. baltica* and *N.hyalina* were unaffected (Rojo et al., 2013b). Furthermore, these authors reported that MC acts as an allelopath in the aquatic ecosystem, with stronger and longer-lasting allelopathic effects in charophyte species than in angiosperms (e.g. *M. spicatum*).

Although MCs have been reported as a potent inhibitor of protein phosphatase 1 (PP1) and type 2A (PP2A) in higher plants and animals (MacKintosh et al., 1990), many studies revealed the involvement of oxidative stress in the toxicity of MCs on aquatic plants, which has been manifested by the increase in reactive oxygen species (ROS) and malondialdehyde (MDA) content (Pflugmacher, 2004; Leflaive and Hage-Ten, 2007; Table 2). This leads to cell membrane damage, genotoxicity, or modulation of apoptosis (Ding and Ong, 2003).

It is well known that aquatic plants have developed an antioxidant system involving antioxidant enzymes or free-radical traps (e.g.GSH) as protection from oxidative stress (Jiang et al., 2011). The activities of antioxidant enzymes such as peroxidase (POD), superoxide dismutase (SOD), soluble and microsomal glutathione *S*-transferase (GST), glutathione peroxidase (GPX) and ascorbate peroxidase (APX) increased following exposure of some macrophytes (e.g. *Lemna minor*, *C. demersum*, *Phragmites australis*, Spirodela oligorrhiz, *Vallisneria natans*) to MCs (Mitrovic et al., 2005; Pflugmacher, 2004; Jiang et al., 2011). Glutathione (GSH) has also been influenced by MCs as it is one of the most important non-enzymatic antioxidant during detoxification process through conjugation with absorbed toxins (Pflugmacher et al., 1998; Takenaka, 2001). In this respect, Jiang et al. (2011) found that GSH content of the macrophyte *V. natans* decreased significantly and reached to the minimum value, when the plant was exposed to MC-LR at a concentration of 5 $\mu g\,L^{-1}$. Additionally, MCs can induce cytological and histological alternations in aquatic plants. For instance, MC-LR inhibited the elongation of *C. demersum* shoot tip meristematic cells and the growth of shoots through an alteration in microtubule organization (Szigeti et al., 2010), and caused early aerenchyma formation and lignification in cell walls in *Phragmites australis* plantlets (Mathe et al., 2007). Furthermore, exposure to MCs caused arrest of mitosis in prophase/prometaphase of *Ceratophyllum demersum* (Szigeti et al., 2010), and chromatin condensation in mesophyll cells of *V. natans* (Jiang et al., 2011), and in *P.australis* root tips (Jambrik et al., 2011). Most studies linked such cytoskeletal changes to the inhibition of protein dephosphorylation by MC toxins in aquatic macrophytes (Szigeti et al., 2010; Máthé et al., 2013).

Table 2
Allelopathic activities of cyanotoxins on aquatic plants.

Toxin	Producer (genera)	Exposure toxin concentrations ($\mu g\,L^{-1}$)	Target macrophytes	Mode of action	References
Microcytsin	*Microcystis, Anabaena, Anabaenopsis, Planktothrix, Oscillatoria*	10–200	*Spirodela oligorrhiz,*	Inhibition of plant growth, chlorophyll	Romanowska-Duda and Tarczynska, (2002)
		75–300 1500–20000	*Lemna gibba,* *Lemna minor*	Inhibition of plant growth, chlorophyll, photosynthesis, induction of oxidative stress	Mitrovic et al. (2005), Saqrane et al. (2007)
		0.1–5 10–20000	*Ceratophyllum demersum*	Inhibition of plant growth, chlorophyll and photosynthesis, induction of oxidative stress, Cytoskeletal and developmental alterations	Pflugmacher, (2002), Pflugmacher (2004) Szigeti et al. (2010)
		1–16 100–4300	*Myriophyllum Spicatum*	Inhibition of plant growth, chlorophyll, photosynthesis Induction of oxidative stress	Rojo et al. (2013b), Yi et al. (2009)
		1–40000	*Phragmites australis*	Growth inhibition, histological alterations, modulate nuclease activity	Mathe et al. (2007), Jambrik et al. (2011)
		1500–15000	*Wolffia arrhiza*	Inhibition of plant growth, induction of oxidative stress	Mitrovic et al. (2005)(2005)
		0.1–25	*Vallisneria natans*	Growth inhibition, seedling reduction, ultrastructural alterations	Yin et al. (2005), Jiang et al. (2011)
		1–16	*C. aspera, C. hispida*	Inhibition of plant growth, chlorophyll, photosynthesis	Rojo et al. (2013b)
Cylindrospermopsin	*Cylindrospermopsis, Aphanizomenon, Umezakia, Raphidiopsis, Anabaena*	25–400	*Hydrilla verticillata*	Inhibition of plant growth, chlorophyll, photosynthesis, induction of oxidative stress	Kinnear et al. (2008)
		500–40 000	*Phragmites australis*	Growth inhibition and histological alterations	Beyer et al. (2009)
		10–20000	*Lemna minor, Wolffia arrhiza*	inhibits growth and modulates protease activity	
Anatoxin-a	*Anabaena, Aphanizomenon, Cylindrospermopsis, Planktothrix, Oscillatoria*	0.005–5	*Ceratophyllum demersum*	Growth inhibition, reduction of photosynthetic pigments, induction of oxidative stress	Ha and Pflugmacher (2013), Ha et al. (2014)
		5–25	*Lemna minor*	Inhibition of plant growth, chlorophyll and photosynthesis, induction of oxidative stress	Mitrovic et al. 2004

Most studies of allelopathic effects of MCs on aquatic plants were conducted at very high concentrations, i.e. up to the mg/L range (see Table 2), beyond environmentally relevant ones which very rarely exceed 15 $\mu g\,L^{-1}$ (Rojo et al., 2013b), with the objective of confirming or rejecting the allelopathic activities of these toxins against aquatic plants. However, some studies displayed minor (LeBlanc et al., 2005; Mitrovic et al., 2005) or harmful effects of MCs on some aquatic macrophytes within environmentally relevant concentrations (Pflugmacher, 2002, 2004). For short term periods, high concentrations of dissolved MCs have occusionally been reported in some eutrophic lakes reaching up to 1800 $\mu g\,L^{-1}$ upon the collapse of toxic blooms and toxin release (Svrcek and Smith, 2004). However, although many studies of MC-concentrations in the filed do include the dissolved fraction, such findings of high dissolved MC-concentrations are rare, probably because once released form cyanobacterial cells, MC is very rapidy biodegraded and also diluted in natural waterbodies. Therefore, aquatic plants may be exposed to such high MC concentrations only briefly during lysis events, and this limits opportunities for their negative effects on plant growth and physiological processes. In contrast to MCs, CYN is apparently actively released from cyanobacterial cells (extracellular) (Saker and Griffiths, 2000), and can persist for long periods in the aquatic environment (McGregor and Fabbro, 2000). This property is of particular concern for the toxicity of CYN as the extracellular fraction would be the most bioavailable to macrophytes. CYN uptake into cells may occur by diffusion because of its low molecular mass (415 Da) (Chong et al., 2002). CYN affects the plants in different ways including inhibition of protein and glutathione synthesis (Runnegar et al., 1994). Kinnear (2010) found that *C. raciborskii* extract containing 0.4 $\mu g\,ml^{-1}$ CYN increased the root growth and decreased chlorophyll content of the macrophyte *Hydrilla verticillata.* Jambrik et al. (2011) demonstrated that CYN caused growth inhibition and modulated the protease activity of the aquatic plants *Lemna minor* and *Wolffia arrhiza* at concentration of 0.01–1 $\mu g\,ml^{-1}$. Furthermore, CYN can induce alterations of root histology and microtubule organization in the common reed *Phragmites australis* at concentrations of 0.5–40 $\mu g\,ml^{-1}$.

In addition to cyanobacterial hepatotoxins, some cyanobacterial neurotoxins can also affect multiple levels of biological metabolism (e.g. growth, photosynthesis and enzymatic systems) of aquatic macrophytes (Ha et al., 2014). Mitrovic et al. (2004) revealed that the exposure of the floating aquatic macrophyte *Lemna minor* to high concentrations of anatoxin-a (5–25 $\mu g\,ml^{-1}$) led to a decrease in photosynthetic oxygen production and increase in peroxidase and glutathione S-transferase activities in these plants. Recently, it has been reported that anatoxin-a can exert phytotoxic effects at environmentally relevant concentrations (0.005–50 $\mu g\,L^{-1}$) on the submerged aquatic macrophyte *Ceratophyllum demersum* (Ha and Pflugmacher, 2013; Ha et al., 2014). Although the mechanism of action of anatoxin-a in mammals has been elucidated as a powerful postsynaptic de-polarizing agent that can bind to nicotinicacetylcholine receptors (nAChRs) in neurons, the metabolism and fate of this neurotoxin have not been well understood in aquatic plants, which are known to have no acetylcholine (Ach) mechanism. However, a recent study by Ha and Pflugmacher (2013) indicated that anatoxin-a can disrupt homeostasis of *C. demersum* through induction of oxidative stress. No data on toxic effects of other cyanotoxins on the aquatic plants is available in the literature yet.

4. Bioaccumulation and biotransformation of cyanotoxins by macrophytes

Despite negative effects of cyanotoxins on aquatic plants, these plants may adapt and develop a resistance to these toxins through accumulation and biotransformation processes (Ha and Pflugmacher, 2013). Several studies have demonstrated the accumulation of MCs in different aquatic macrophytes (Table 3).Yin et al. (2005) revealed the accumulation of MCs in both roots and leaves of *V. natans* to concentrations ranging from 0.3–15 $\mu g\, g^{-1}$.The emergent reed plant P. australis was found to accumulate MC-LR in the stems and rhizomes (Pflugmacher et al., 2001). In addition, *L. minor* has also been shown to accumulate MCs up to a concentration of 0.11 $\mu g\, g\text{-}^{1}$ (Mitrovic et al., 2005), while *L. gibba* accumulated MCs to a concentration reaching 2.24 $\mu g\, g^{-1}$ (Saqrane et al., 2007). Recently, *Hydrilla verticillata* was found to accumulate MCs with bioconcentration factor of 16 (Romero-Oliva et al., 2014). For CYN, there are a few studies on the accumulation of this cyanotoxin in aquatic plants. Only *Lemna punctata* was found to accumulate CYN with high bioconcentration factor (BCF = 86.67) (Seifert 2007).Conversely, *Hydrilla verticillata* did not exhibit any CYN accumulation in its tissues, even with exposure concentrations up to 400 $\mu g\, L^{-1}$ (White et al., 2005). Kinnear et al. (2007) also reported the absence of CYN accumulation in the duckweed *Spirodela oligorrhiza.* In addition to hepatotoxins, the accumulation of the neurotoxin Anatoxin-a was also observed in *C. demersum*, and the level of this toxin in the plants exhibited a concentration-dependent increase with average value of 15.84 ng g FW^{-1} obtained at the highest exposure concentration, 50 $\mu g\, L^{-1}$ (Ha et al., 2014). More recently, Kaminski et al. (2015) revealed that *Lemna trisulca* accumulated anatoxin-a inside its tissues (150 $\mu g\, g^{-1}$ DW) on day 4 of its co-cultivation with anatoxin-a-producing *Anabaena flos-aquae*. Like other aquatic organisms (e.g. fish & mussels), macrophytes are able to biotransform xenobiotics including cyanotoxins into less phytotoxic compounds (Tangahu et al., 2011; Ha and Pflugmacher, 2013).The biotransformation pathways involves the change of these toxins into another forms by cytochrome P-450 monooxygenases (phase I), conjugation with glutathione via glutathione *S*-transferases (phase II), and finally phase I and phase II metabolites. Animals excrete these metabolites through their excretory systems and may deposite them in vacuoles or cell wall fractions (Pflugmacher et al., 2001).The biotransformation of MCs has been reported by several authors in some aquatic macrophytes (e.g., C .demersum, *Phragmites australis, Lemna gibba*, *L. minor*, *Spirodela intermedia, H. verticillata*) (Pflugmacher et al., 2001; Ferreira et al., 2009; Saqrane et al., 2007; Romero-Oliva et al., 2014).Those authors have concluded that the biotransformation pathway of MCs in aquatic plants starts by the formation of MC-glutathione conjugate by the activity of glutathione-S-transfers, this conjugate is then further metabolized and converted into a MC-cysteine conjugate by carboxypeptidase, and finally cysteine conjugate is oxidized through acetyl transferase, forming the microcystin-LR-mercapturic acid conjugate. These metabolites, being water soluble are exported out of the cells into vacuoles or deposited into the cell wall compartments such as lignins resulting in a compartimentation for nontoxic long time storage (Sandermann, 1992).

For other cyanotoxins, no data are available on their biotransformation pathways in aquatic plants, but hypotheses have been proposed. For instance, White et al. (2005) explained the apparent lack of bioconcentration of CYN in the macrophyte *H. verticillata* by the possible metabolism of this toxin through enzymatical conjugation or nonenzymatical binding to intracellular reduced glutathione (GSH) in a similar way as MCs. Similarly, the decrease in the maximum amount of anatoxin-a detected in exposed *Ceratophyllum demersum* plants after 24 h within the following 336 h of exposure suggests the metablization of this toxin in the plant (Ha et al., 2014). Recently, Kaminski et al. (2014) showed that the metabolism of anatoxin-a *in L. trisulca* occurrs through its transformation to simple products (50 Da), or absorption of some of the toxin molecules by unknown molecules in the plant.

5. Examples of demonstrated control of cyanobacterial blooms by macrophytes in mesocosm scale or field experiments

Proving an allelopathic inhibition of phytoplankton, particularly of cyanobacteria by macrophytes in the field still remains unclear and controversial (Gross et al., 2007; Hilt and Gross, 2008). Most of the existing research was carried out in lab scale using plant extracts, exudates or purified compounds. However, there have been some mesocosm and field experiments testing macrophyte effects on phytoplankton as a way of controlling harmful cyanobacterial blooms. A filed study by Hilt et al. (2006) revealed the inhibitory allelopathic effects of the macrophyte *M. verticillatum* on phytoplankton including cyanobacteria under *in situ* conditions (Lake Krumme Laake, Berlin, Germany). The authors showed that potentially confounding parameters like water temperature, pH and oxygen content did not differ significantly between the control and the *M. verticillatum* stands in most cases, and thus the effects observed could indeed be attributed to *M. verticillatum*. An *in situ* incubation experiment in the Danube Delta, Romania, demonstrated that the growth rate of natural phytoplankton populations exposed to water from *S. aloides* stands was significantly lower than that of populations that had not been in contact with *S. aloides* exudates (Mulderij et al., 2006). Declerck et al. (2007) detected a strong inhibition of phytoplankton growth by the macrophyte *Elodea nuttallii* in a mesocosm study at high nutrient levels that could not be explained by the mere structure of the plants as shown by using artificial plants.Vanderstukken et al. (2011) carried out a mesocosm experiment to investigate the influence of macrophytes on phytoplankton excluding the effects of competition for nutrients and zooplankton grazing. They found that the tested macrophytes species (*Egeria densa* and *Potamogeton illinoensis*) were able to suppress phytoplankton growth through allelopathic activities. Conversely, a comparison study of unplanted and planted microcosms in Guishui Lake, China with submerged macrophytes (*Lindernia rotundifolia, Hygrophila stricta,* and *Cryptocoryne crispatula*) showed that the primary mechanism suppressing a cyanobacterial bloom in the planted microcosms was the decrease in nutrient concentrations caused by macrophytes (Wang et al., 2012). Recentely, an *in situ* experiment in Chaohu Lake, China, revealed that the combination of *Nymphoides peltatum,* which has allelopathic potential, with a zooplankton community showed a 1.6–3.8-fold increase of the inhibition rate of harmful water-bloom microalgae compared to the effect of the macrophyte or the zooplankton (i.e.grazing) alone (Zuo et al., 2015). The authors suggest that allelopathic macrophtes and predatory zooplankton may have interacted in their effects of algal growth., e.g. the macrophytes may have improved the habitat for zooplankton, thus facilitating grazing on phytoplankton. The authors also reported that eutrophication of shallow lakes would weaken algal inhibition (i.e. reduction in cell numbers) due to grazing by herbivorous zooplanktons and allelopathic macrophytes, e.g. through adverse effects of hypoxia and changes in pH on populations of grazing zooplankton (Zuo et al., 2015). Furthermore, Švanys et al. (2014) found that the presence of *Myriophyllum spicatum* in mesocosms (Curonian Lagoon) reduced the biomass of both microcystin-producing and non-microcystin-producing *M. aeruginosa* populations in a natural phytoplankton community under hypertrophic conditions. On the other hand, Lombardo et al. (2013) concluded that competition for nutrients

Table 3
Bioaccumulation and biotransformation of cyanotoxins by macrophytes.

Toxin	Target macrophytes	Bioacuumulation	Biotrasformation	References
Microcytsin	*Eichhornia crassipes*	16.9 μg g^{-1} DW*	Possibly transformed	Romero-Oliva et al. (2014)
	Spirodela intermedia	0.065 μg g^{-1} FW*	Glutathione conjugate/cysteine conjugate	Ferreira et al. 2009
	Lemna gibba,	0.29- 2.24 μg g^{-1} DW	Microcystin-glutathione-conjugate/	Mitrovic et al. (2005), Saqrane et al.
	L. minor	0.046- 8.68 μg g^{-1}FW	Microcystin −cysteine-conjugate	(2007), Wang et al. 2012
	Ceratophyllum demersum	1.98 μg g^{-1} FW	glutathione-toxin conjugate	Pflugmacher et al. 1999, Pflugmacher, 2004
	Phragmites australis	0.135 μg g^{-1} FW	Glutathione conjugate/cysteine conjugate	Pflugmacher et al. 2001, Jambrik et al. (2011)
	Polygonum portoricensis	583 μg g^{-1} DW	Possibly transformed	Romero-Oliva et al. (2014)
	Typha sp.	1.65 μg g^{-1} DW	Possibly transformed	Romero-Oliva et al. (2014)
	Vallisneria natans	15.1 μg g^{-1} FW	Not investigated	Yin et al. (2005), Jiang et al. (2011)
	Hydrilla verticillata	14.5 μg g^{-1} DW	Possibly transformed	Romero-Oliva et al. (2014)
Cylindrospermopsin	*Hydrilla verticillata*	Absence of accumulation	Possibly detoxified by binding to phytochela-tins synthesized by plant in response to the toxin	White et al. (2005), Kinnear et al. 2008
	Spirodela oligorrhiza	Absence of accumulation	Not investigated	Kinnear et al. (2007)
	Lemna punctata	BCF = 86.67	Not investigated	Seifert et al. (2007)
Anatoxin-a	*Ceratophyllum demersum*	15.84 ng g FW^{-1}	Possibly transformed as the accumulating toxin was reduced along the time	Ha et al. (2014)
	Lemna trisulca	150 μg g^{-1} DW	Possibly transformed to simple products (50 Da), or might have been absorbed by unknown molecules in the plant	Kaminski et al. (2014, 2015)
	Myriophyllum spp.	0.18-8.4 μg g^{-1} DW	Not investigated	Al-Sammak et al. (2014)

DW = dry weight, FW = Fresh weight.

and/or allelopathy does not seem to be primary factor involved in *in situ* macrophyte–phytoplankton patterns in two Norwegian lakes. They suggested that *in situ* macrophyte–phytoplankton patterns may be strongly influenced by factors operating at a large scale such as lake trophic state and extent of submerged vegetation coverage.

6. Conclusions and potential for developing bloom control through macrophytes

Based on the information recounted above, it is clear that some aquatic macrophytes can support the restoration of eutrophic water bodies and might have the ability to control cyanobacterial growth through allelopathy and/or utilization of large amounts of nutrients. However, critical questions need to be addressed desgining or developing strategies for bloom control by macrophytes at ecosystem level. Among these questions are which macrophyte species are suitable for cyanobacterial bloom control in the specific situation, whether macrophyte allelochemicals can be expected to be released in sufficient amounts to have an effect, whether the lake is of a type in which macrophytes or their extracts have chances for successful bloom control, whether the allelopathic macrophytes chosen selectively inhibit cyanobacteria and not also other phytoplankton (with a positive role in the ecosystem), and which environmental factors may influence macrophyte allelopathic effects on cyanobacteria.

During the last decade, substantial research efforts have been directed to explore these questions. Based on the results of many studies, the selection of macrophyte species for bloom control depends on the dominance and successful survival of allelopathically active species in lakes under eutrophic conditions (Hilt and Gross, 2008; Blindow et al., 2014). For instance, charophytes dominate at lower nutrient concentrations and can develop higher areal biomass than angiosperms which dominate at high nutrient concentrations (Hilt, 2015). Furthermore, Meerhoff and Jeppesen (2010) and Albertoni et al. (2014) proposed that floating macrophytes could be grown in tropical and subtropical shallow lakes at high nutrient levels. Scheffer et al. (2003) also provided field evidence that free-floating macrophytes showed a positive correlation to nutrient levels of the water column, whereas submerged plants were negatively related to nutrient levels. Regarding the type of lake in which planting macrophytes is likely to be successful it has been reported that macrophytes might have allelpathic effects in shallow lakes if macrophytes occupy a substantial part of the littoral zone of these lakes (Bauer et al., 2009; They et al., 2015). The most important reason is that the concentrations of allelochemicals achieved by release from aquatic macrophytes in natural aquatic ecosystems are much lower than in the lab and cannot reach the 50% inhibitory concentrations (EC_{50}) required to inhibit phytoplankton growth (Nakai et al. 2000; Hilt et al. 2006).In this context, it has been reported that significant allelopathic effects on phytoplankton occur when macrophyte biomass densities are approximately 80–800 g dry weight m $^{-2}$ in water of 1 m depth (Körner and Nicklisch, 2002; Nakai et al., 1999), and the biomass of submerged macrophytes in shallow eutrophic lakes can easily exceed these values (Hilt and Gross, 2008). Another key point which should be taken into account if evaluating ecological consequences of allelopathic interactions is that the allelochemical should selectively inhibit the harmful target organisms without any adevrese effects on the community structure of the aquatic ecosystems. Fortunately, most studies found that phytoplankton species exhibit variable sensitivities to macrophyte allelochemicals, with cyanobacteria as the most sensitive group, while green algae are known to be less sensitive (Mulderij et al., 2007; Hilt and Gross, 2008; Mohamed and Al Shehri, 2010).

Besides the control of growth of harmful cyanobacteria, macrophytes could be also used as phytoremediators for elimination of cyanotoxins from water bodies.This is due to the ability of some macrophytes to take up cyanotoxins and to adjust their metabolisms and biotransform them to less toxic or even nontoxic compounds as outline above. Because of such biotransformation capacity, macrophytes could be regarded as the green liver, based on the fact that both mammals and plants exhibit a similar mechanism for the metabolisation of toxic compounds (Nimptsch et al., 2008). The green liver concept was applied in an experimental pond system by using some macrophytes (e.g. *Hydrilla* sp., *Lemna* sp. & *Myriophyllum* sp.) to remove MC toxins from drinking water sources via bioaccumulation in the plants as a preliminary purification step

before entering water treatment plants (Nimptsch et al., 2008). Taken that exposure of aquatic plants to high concentrations of cyanotoxins exerts deleterious effects leading to plant death, lysis and potential release of accumulatied toxins into the water, the latter authors suggested the removal of aquatic plants from the pond system before they die off. Additionally, these plants containing accumulated toxins should be stored away from the water body – on land, protected from children until monitoring shows that this plant debris is no longer realeasing toxins.

A further issue to consider when planting macrophytes as green liver to remove cyanotoxins via bioaccumulation in lakes and rivers is that in larger natural settings they can scarcely be regularly removed. In temperate settings and where cyanotoxin concentratons are not expected to be so high that they will kill the macrophytes, die-off would occur at the end of the growing season, and removal only then – i.e. only once – might suffice. A further concern raised is that macrophytes may transfer the cyanotoxins via bioaccumulation along the aquatic food chain (Pflugmacher, 2004) as primary producers offering food to other organisms at different trophic levels. For these reasons, it is preferable to apply the green liver concept in permanent and large water bodies through using macrophytes with cyantoxin biotransformation capability (e.g. *Ceratophyllum demersum, Phragmites australis, Spirodela intermedia, H. verticillata*) but not by macrophytes with bioaccumulation capacity (e.g. *Lemna* sp., *Myriophyllum* sp. and *Hydrilla* sp.)

Conflict of interest

The author declares that there is no any kind of conflict of interest.

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