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VARIATIONS OF MICROCYSTINS IN FRESHWATER ECOSYSTEMS

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Abstract

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Increased frequency, severity of harmful algae blooms and their extent worldwide have become a global challenge due to the production of toxins that are released to the water. Cyanotoxins are detected in 25–75% of blooms. Hazardous hepatotoxin-microcystin potential producers, spatial and temporal variations of toxins as well as their variations depending on environmental variables are discussed in this overview. The most common species among microcystin producers belong to the genera *Dolichospermum* and *Microcystis*. Variations of the amount of microcystins detected through the bloom are associated with the dominant cyanobacteria species or its genotype. The abundance of toxic cyanobacteria genotype and cyanotoxin values increase with the rise of water temperature and nutrient concentrations in the freshwaters. On the seasonal basis, cell-bound microcystin concentrations increase with bloom development, whereas extracellular cyanotoxin values rise with the senescing of bloom after cyanobacterial cell lysis.

Keywords: HABs, cyanobacteria, cyanotoxins, environmental variables, freshwaters.

INTRODUCTION

Harmful algae blooms (HABs) have been recorded in over sixty countries worldwide and have become a global problem, because the cyanotoxins have been detected in 25–75% of blooms (Chorus, 2001; Svrcek & Smith, 2004; Pan et al., 2011). Microcystins (MC) are the commonly detected cyanotoxins in freshwater ecosystems having the broadest variety (up to 90) of known isoforms (Sivonen & Jones, 1999). Cyanobacteria from the genera *Microcystis, Dolichospermum, Nostoc, Planktothrix* and *Oscillatoria* are known as hepatotoxin-microcystin producers. In Europe, the comprehensive surveys of cyanobacterial blooms in Belgium, Luxembourg and France have revealed that microcystins were found in 53% of the analysed blooms and microcystin-LR (MC-LR) was the most common isoform (Willame et al., 2005).

The ability to produce toxins can change temporally and spatially at a particular water body (Ressom et al., 1994) and concentrations of dissolved MC in the environment may vary from traces up to 1800 μg L^{-1} or higher (Chorus & Bartram, 1999). Microcystin isoforms within one cyanobacteria strain may range up to 11, the concentration up to 4.799 μg g^{-1} of dry weight (Krüger et al., 2010). The overall concentration of MC in a bloom is determined by both the cellular rates of MC production and community dynamics of cyanobacterial populations. Cellular MC production has been indirectly linked to environmental factors influencing cyanobacterial growth rates (Orr & Jones, 1998), which can account for a 3–4-fold variation in total MC concentrations (Kurmayer et al., 2002, 2003). The toxicity of a single bloom may, however, change in both time and space. So, understanding of the environmental factors associated with cyanobacterial bloom formation, the occurrence of MC produc-

ing species and MC production is an essential step to predict toxic events (Hotto et al., 2008). Cyanotoxins represent a potential health risk for humans when occurring in freshwaters used for drinking water supply, recreation and irrigation. Hundell (2010) emphasised that the primary importance should be concentrated on the incidence of cyanobacterial blooms, the types and quantities of cyanotoxins most commonly produced as well as on integrated assessment of health and ecological effects of cyanotoxin mixtures.

An objective of this overview was to discuss potential hepatotoxin-microcystin producers, spatial and temporal variations of microcystins as well as the variations of toxins depending on environmental variables.

POTENTIAL MICROCYSTIN PRODUCERS, TOXIC AND NON-TOXIC CYANOBACTERIA GENOTYPES

Microcystins have been isolated from multiple genera of cyanobacteria. Cyanobacteria from 25 genera are known to produce MC (Table 1). Most of these cyanobacteria are bloom and scum-forming species that have a cosmopolitan distribution (Codd et al., 1999; Pearson et al., 2010; Sainis et al., 2010). The most common species among the MC producers belong to the genera *Dolichospermum* and *Microcystis,* and frequently form hepatotoxic blooms worldwide. Co-occurring cyanobacterial populations and species in lakes and reservoirs may produce very complex toxin profiles (Namikoshi et al., 1995). In a single *Microcystis* bloom up to 19 microcystin isoforms have been observed. Although many strains produce several MC congeners simultaneously, usually only one or two isoforms are dominant in any single strain. Moreover, seven cyanobacteria species, in addition to MC, may produce other hepatotoxins or neurotoxins (Table 1).

Cyanobacteria species differ in the toxicity by having or not specific genes for cyanotoxin synthesis. Microcystin synthetase genes (*mcy*) were detected in 73% of *Microcystis aeruginosa* colonies from Lake Wannsee, 16% of *M. ichthyoblabe* and none in *M. wesenbergii* colonies (Kurmayer et al., 2002). Similarly, Via-Ordorika et al. (2004) found that the frequency of *mcy* genes varied in different *Microcystis* morphospecies collected from the lakes across Europe. More than 75% of *M. aeruginosa* and *M. botrys* colonies contained the *mcy* genes, whereas only 20% of *M. ichthyoblabe* and *M. viridis* colonies gave a PCR product of the *mcy* genes. *Mcy* genes were not found in *M. wesenbergii*. Consequently, seasonal

Table 1. Microcystin-producing cyanobacteria species*

Cyanobacteria species
Anabaenopsis millerii V.V.Miller
Aphanizomenon flos-aquae Ralfs ex Bornet & Flahault **(ANTX-a, CYL, STX)**, ***A. ovalisporum*** Forti **(CYL)**
Aphanocapsa cumulus Komárek & Cronberg
Arthrospira fusiformis (Voronikhin) J.Komárek & J.W.G.Lund
Cyanobium bacillare (Butcher) Komárek, Kopeck & Cepák
Dolichospermum circinale (Rabenhorst ex Bornet & Flahault) P.Wacklin, L.Hoffmann & J.Komárek **(STX)**, ***D. flosaquae*** (Brébisson ex Bornet & Flahault) P.Wacklin, L.Hoffmann & J.Komárek **(ANTX-a, ANTX-a(s))**, ***D. lemmermannii*** (Ricter) P.Wacklin, L.Hoffmann & J.Komárek **(STX, ANTX-a(s))**, *D. viguieri (Denis & Frémy) Wacklin, L.Hoffm. & Komárek*
Haphalosiphon hibernicus West & G.S.West
Leptolyngbya boryana (Gomont) Anagnostidis & Komárek
Limnothrix redekei (van Goor) M.-E.Meffert
Merismopedia tenuissima Lemmermann
Microcystis aeruginosa (Kützing) Kützing **(ANTX-a)**, *M. flos-aquae* (Wittrock) Kirchner, *M. viridis* (A.Braun) Lemmermann, *M. botrys* Teiling, *M. ichthyoblabe* (Kunze) Kützing, *M. novacekii* (Komárek) Compère, *M. panniformis* J.Komárek, J.Komárková-Legnerová, C.L.Sant'Anna, M.T.P.Azevedo, & P.A.C.Senna
Nostoc linckia (Roth) Bornet, *N. paludosum* Kützing ex Bornet & Flahault, *N. rivualre* Kützing, *N. spongiaeforme* C.Agardh, *N. zetterstedtii* Areschoug
Oscillatoria limosa C.Agardh ex Gomont, *O. perornata* Skuja
Phormidium formosum (Bory de Saint-Vincent ex Gomont) Anagnostidis & Komárek
Planktothrix agardhii (Gomont) Anagnostidis & Komárek, *P. mougeoti* K.Anagnostidis & J.Komárek, ***P. rubescens*** (De Candolle ex Gomont) Anagnostidis & Komárek **(ANTX-a)**
Trichodesmium erythraeum Ehrenber,*T. thiebautii* Gomont
Snowella lacustris (Chodat) Komárek & Hindák
Other cyanobacteria genera known as microcystin producers: *Chroococcus, Fischerella, Plectonema, Pseudanabaena, Radiocystis, Synechococcus, Synechocystis, Woronichinia*

Species **in bold** – able to produce other cyanotoxins; abbreviations: ANTX-a – anatoxin-a, ANTX-a(s) – anatoxin-a(s), CYL – cylindrospermopsin, STX – saxitoxins.
* after Chorus, Bartram, 1999; Figueredo et al., 2004; Zurawell et al., 2005; etc.

variation in abundance of *Microcystis* species result in significant differences in MC net production and total concentration (Park et al., 1993; Harada et al., 2001; Kurmayer & Christiansen, 2009). *Mcy*-genotype proportion in the *Microcystis* population was found to vary on a seasonal scale from 1 to 38%, but the average proportions during vegetation season were found to be fairly constant (Kurmayer & Kutzenberger, 2003; Sabart et al., 2010). Kurmayer & Gumpenberger (2006) found that the spatial isolation of populations rather than the seasonal influence of biotic or abiotic factors leads to differences of MC-producing genotypes in the cyanobacteria population (Okello et al., 2010 and references therein).

On the other hand, microcystin production varies greatly between different strains of the same species (Li et al., 2009) and between clones from the same isolate (Carmichael, 1992). The MC concentration in the bloom is strongly related to the proportion or cell number of toxic genotypes (Kurmayer et al., 2003; Joung et al., 2011). Genotype diversity between strains has been posed as the main factor determining the variability in toxicity levels in blooms of the same species, with the development and success of strains better adapted to certain environmental conditions (Figueiredo et al., 2004). The tremendous variability in toxin level in cyanobacterial blooms is suggested to be due to the successive replacement of toxigenic and nontoxigenic strains, which can determine over a 30-fold variation in MC concentrations (Kardinaal & Visser, 2005).

Nontoxic-, and highly toxic *Microcystis* strains coexist in a single bloom and their relative proportions vary depending on environmental factors (Sivonen & Jones, 1999; Kurmayer et al., 2003; Rinta-Kanto & Wilhelm, 2006; Krüger et al., 2010; Joung et al., 2011). Nontoxic *Microcystis* may have some ecological advantages over toxic strains under normal conditions. According to Joung et al. (2011), non-toxic *Microcystis* was generally dominant over potentially toxic genotypes, while the toxic predominated briefly during the bloom. Dominance of toxic and nontoxic strains is likely to depend on a combination of the strain characteristics and environmental factors. The proportions of toxic *Microcystis* genotypes have been related to nutrient concentrations (Yoshida et al., 2007; Rinta-Kanto et al., 2009). Rantala et al. (2006) and Te & Gin (2011) reported that the total nitrogen and total phosphorus concentrations were related to the microcystin-producing genera and microcystin concentrations, respectively. Thus, an increase of toxic genotypes depends on the eutrophication degree of the water ecosystem. The transient dominance of toxic *Microcystis* over nontoxic seems to be strongly related to the higher water temperature also (Joung et al., 2011). Water temperature rather than the total phosphorus (TP) amount influence the *Microcystis* bloom toxicity, because the high TP concentration induces growth of both toxic and nontoxic genotypes. Experiments conducted by Davis et al. (2009) also showed that elevated water temperature enhanced the growth rate of toxic *Microcystis* more than non-toxic. Wilhelm et al. (2011) found that temperature was ~4°C higher in the lake stations with maximum values of cyanotoxins, nevertheless, no strong relationship between surface temperature and toxin concentrations was found. So, according to Wilhelm et al. (2011) and Joung et al. (2011), the TP concentration was the fundamental regulating factor for *Microcystis* proliferation, whereas water temperature was more closely related to the proportion of toxic cyanobacteria genotypes. It was suggested that eutrophication and global warming together could lead to the increase in frequency of toxic blooms (Paerl & Huisman, 2008; Davis et al., 2009). The proportion of toxigenic *Microcystis* cells in tropics is much higher (22–100%) compared to subtropical and temperate regions (e.g. up to 38.3%, Kurmayer & Kutzenberger, 2003; up to 35%, Mitsuhiro et al., 2007; 8.5–17.7%, Rinta-Kanto et al., 2009; up to 27%, Baxa et al., 2010; Te & Gin, 2011 and references therein). The relatively low proportion of *mcy* genotypes in *Microcystis* that can be observed across the Northern hemisphere implies that only a small part of *Microcystis* populations are of relevance for the MC net production in lakes (Kurmayer et al., 2003; Hotto et al., 2008). Nevertheless, Sabart et al. (2010) recorded 70–100% of potentially MC-producing cells (*mcy*B genotype) in *M. aeruginosa* populations from lake in France.

SPATIAL AND TEMPORAL MICROCYSTIN VARIATIONS

Harmful cyanobacteria blooms are typically patchy, even in small areas such as bays and coves in small lakes. Thus, cells amount and toxin concentrations of

cyanobacteria can be significantly different from one site to another, particularly in open water (Backer et al., 2010). The largest cyanobacteria formations were observed in the morning before winds developed and in the embayments. Later in the day when wind and wave action increased, cells accumulate near the shoreline. Makarewicz et al. (2009) recorded considerable variability in MC-LR concentrations in different habitats within Lake Ontario. In general, the average MC-LR concentration was two orders of magnitude lower in embayment, river and shore side sites compared to upland lakes and ponds. The highest cyanotoxin concentrations were typically reported in the upper one meter layer (Utkilen & Gjolme, 1992; Murphy et al., 2003), however, metalimnetic populations of potential MC-producing cyanobacteria occasionally bloom at depth, particularly in mesotrophic systems (Lindholm, 1991; Graham et al., 2008).

Microcystin concentrations also vary throughout the bloom period. In Lake Ontario, MC-LR concentrations were low in May, increased over the summer, and reached the maximum in September (Makarewicz et al., 2009). Similarly, Rogalus & Watzin (2008) reported that MC concentrations were the lowest in early bloom period, then increased and stabilized with the establishment of the bloom. The significant effect of bloom stage on MC concentration suggests that bloom development favours a rise in the proportion of MC-producing cyanobacteria. In the aquatic ecosystems, healthy bloom populations apparently produce small amount of extracellular toxins (Li et al., 2009), whereas concentrations of cell bound MC are several orders of magnitude higher. Only negligible amounts of toxins are apparently excreted from healthy cells, whereas MC is released after cell lysis (Sivonen & Jones, 1999). So, high concentrations of dissolved MC could be reached in water immediately after the collapse of a toxic bloom. Li et al. (2009) experimentally showed that the concentrations of extracellular MC in the medium were the lowest at the initial growth phase of cyanobacteria and release to the water phase increased subsequently when the cells began to decay.

Dittmann et al. (2001) suggested that MC may regulate population behaviour such as aggregation into colonies within the ongoing seasonal cyanobacteria development. Unicells and small colonies (cell number < 20) dominated among the recruited *Microcystis aeruginosa* untill mid-April, whereas colonies with cell number higher than 200 started to develop from June (Cao & Yang, 2010). According to Misson et al. (2011), most of the recruited *Microcystis* colonies were larger than 160 μm, but cells contained ten times greater amounts of MC than those in the sediments. They found that the recruitment of the smallest and the most toxic subpopulations was governed by temperature and light conditions. Other studies showed that MC production increases with the increase in *Microcystis* colony size during the blooms (Kurmayer et al., 2003; Via-Ordorika et al., 2004; Rogalus & Watzin, 2008; Wang et al., 2013). Colonies of *Microcystis* larger than 100 μm showed the highest percentage of MC-producing genotypes and MC cell quotas (Kurmayer et al., 2003; Wang et al., 2013). Moreover, colonies with size of more than 100 μm showed higher proportion of the most toxic congener MC-LR than the colonies with lower size (Wang et al., 2013). The latter study demonstrated that toxic/non-toxic genotype composition and isoforms of MC in the different *Microcystis* colonies size groups resulted the variations of MC production.

MICROCYSTIN VARIATIONS DEPENDING ON ENVIRONMENTAL VARIABLES

The regulation of toxin net production has been addressed by a number of studies that quantified the effects of various environmental conditions on the toxin content for individual strains in the laboratory (Kurmayer & Christiansen, 2009). A wide range of physiochemical variables (e.g. temperature, irradiance, macronutrients, trace elements, salinity, CO_2 and pH) can affect toxin production and the growth of different cyanobacterial genotypes by a factor, but no more than three to four (WHO, 1998; Briand et al., 2009). Toxins production in cyanobacteria increases at a high nutrient concentration, light intensity, temperature, dissolved oxygen concentration and pH (Jacoby et al., 2000; Katircioğlu et al., 2004; Sekadende et al., 2005; Wu et al., 2006; Te & Gin, 2011), however, no single variable can fully describe the formation of blooms or the synthesis of toxins (Graham et al., 2004).

Microcystin synthesis increases at high light intensity or photosynthetically active radiation (Figueiredo et al., 2004; Pearson et al., 2010) and light quality is

also a determinant factor. An increased transcription of *mcy* genes under high light (68 μmol m^{-2} s^{-1}) intensity and red light was documented, while the transcription rates reduced under 16 μmol m^{-2} s^{-1} light intensity and dark conditions (Kaebernick et al., 2000; Kurmayer & Christiansen, 2009). Blue light reduced the *mcy* transcription; however, it was not ceased. Laboratory experiments showed that MC content increased until the light intensity levels that can reach in the epilimnion at the high intensities of solar radiation (Kaebernick et al., 2000; Wiedner et al., 2003). Light intensity appears to favour the production of certain MC variants over the others (Tonk et al., 2005). The microcystin isoform MC-DeRR content in *P. agardhii* decreased twofold, whereas the microcystin isoform MC-DeLR increased threefold with the increased photon irradiance; nevertheless, the cellular content of total MC remained constant. High light intensities increase cellular iron uptake, which may be responsible for toxin production (Katircioğlu et al., 2004).

Elevated temperature yield growth of the toxic *Microcystis* cells and/or cells with *mcy*D gene copies per cell, and consequently the toxicity bloom increase (Davis et al., 2009). Temperature was shown to influence the type of toxin produced by *Dolichospermum* spp. High temperatures (> 25°C) enhance MC-RR isoform production and lower temperatures favour MC-LR synthesis (Figueiredo et al., 2004; Katircioğlu et al., 2004). Rapala et al. (1997) reported up to a 30-fold cyanotoxin variation under different temperature conditions, when the growth of the strains was poor.

Under the salinity up to 10 g l^{-1}, the specific growth rate of *Microcystis aeruginosa*, MC cell quota and MC production remained unaffected. Extracellular MC concentrations raised due to cell lysis, when salinity reached 10 g l^{-1} (Orr et al., 2004; Liu, 2006; Tonk et al., 2007). Halinen et al. (2007) and Engström-Öst et al. (2011) noted that toxic strains of *Dolichospermum* were isolated from the Baltic Sea areas with the lower salinities suggesting that low salt concentration may favour MC-producing strains growth.

There are a lot of controversial results concerning the effects of nitrogen and phosphorus concentrations on MC content in cyanobacteria. Vézie et al. (2002) stated that toxins production in *Microcystis* seems to be influenced by variation in nitrogen and phosphorus concentrations with different responses depending on the particular strain. Decreased fivefold amounts of MC were reported under the lowest 0.05 mg L^{-1} phosphorus concentrations (Metting & Pyne, 1986; Sivonen & Jones, 1999). *Dolichospermum, Aphanizomenon, Cylindrospermopsis* strains that are capable to fix nitrogen show high levels on MC concentrations in a nitrogen-free medium, while *Microcystis, Oscillatoria* – in the nitrogen rich enviromnet (Sivonen & Jones, 1999). *Aphanizomenon flos-aquae* toxin production correlates with the age of the culture, temperature and light intensity, but not with the nitrogen (Metting & Pyne, 1986). Briand et al. (2005) noted that environmental variables such as phosphate concentrations have no direct impact on MC production by *P. rubescens*, but act indirectly by affecting growth rate.

Some microelements may influence cyanotoxin production as well. Sevilla et al. (2008) reported interrelationship between the extracellular iron availability and *mcy* transcription rate. Iron starvation implicates slower cell growth, but causes an increase in *mcy*D transcription that correlates to the increase of toxins (Lukac & Aegerter, 1993; Katircioğlu et al., 2004). Lukac & Aegerter (1993) found that remove of iron represented a stress for *M. aeruginosa*, toxin production was not negatively affected, but rather enhanced. However, Li et al. (2009) found that iron concentrations below 5 mM can limit both cyanobacteria growth and all microcystin isoforms (MC-LR, MC-RR, MC-YR) production. Lukac & Aegerter (1993) found that zinc enhanced growth and MC production in *M. aeruginosa*, while Utkilen & Gjlme (1992) obtained contradictory results probably due to the use of a different strain. According to Gouvêa et al. (2008), cellular levels of MC per unit Chl *a* were concomitant with specific growth rather than being triggered in response of ultraviolet radiation, Zn, and Cu stressors alone or in combination. A strong inverse relationship between two MC congeners was observed, where MC-RR increased in contribution to the total toxin pool with the Na concentration, while microcystin isoform MC-LA significantly decreased (Wilhelm et al., 2011). These researches suggested that MC concentrations were correlated to the diversity of the eubacterial community, implying that specific bacteria may associate with bloom events and/or be associated with nutrient sources loading into this system. Orr & Jones (1998) found that MC produc-

tion is controlled by environmental effects on the rate of cell division, not through any direct effect on the metabolic pathways of toxin production. According to them, however, the influence of all environmental factors is indirect, through their effect on cell division and growth, whereas the direct effects on MC biosynthesis are of a relatively minor importance.

In conclusion, microcystin variations in the freshwaters mainly depend on cyanobacteria species and the proportion of toxic genotypes in the populations. Spatial and temporal distribution of toxin is related particularly to ecological species requirements (e.g. optimum temperature, nutrient) and the environmental variables. Variation of water temperature and light intensity determine the toxicity of recruited *Microcystis* colonies. Cell-bound toxicity of cyanobacteria increases with the ongoing bloom, however, toxins mostly are released after the bloom collapse.

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MIKROCYSTINAI GĖLAVANDENĖSE EKOSISTEMOSE

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Santrauka

Toksinus sintetinančių melsvabakterių intensyvus vystymasis lėmė globalius iššūkius žmonijai dėl dažnesnių, didesnio mąsto bei plačiai išplitusių toksinių „vandens žydėjimų“ visame pasaulyje. Cyanotoksinai aptinkami 25–75% „vandens žydėjimų“. Apžvalgoje pateikiamos melsvabakterių rūšys, sintetinančios pavojingus hepatotoksinus mikrocistinus, šių toksinų kiekio kaita laike ir erdvėje, jų kiekio priklausomybė nuo skirtingų aplinkos faktorių. Mikrocystinus dažniausiai produkuoja *Dolichospermum* ir *Microcystis* genčių rūšys. Šių toksinų kiekio svyravimai „žydėjimo“ metu pirmiausiai priklauso nuo melsvabakterių rūšies ar jos genotipo. Toksinių melsvabakterių genotipų gausumas, o taip pat ir mikrocystinų kiekis didėja kylant vandens temperatūrai ir didėjant maismedžiagių kiekiams gėlavandenėse ekosistemose. Ląstelėje surištų mikrocystinų kiekiai didėja formuojantis „vandens žydėjimui“, tuo tarpu vandenyje ištirpusių mikrocystinų kiekiai padidėja „žydėjimo“ pabaigoje, dėl cianobakterijų ląstelių irimo.