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REVIEW

Tropical cyanobacterial blooms: a review of prevalence, problem taxa, toxins and influencing environmental factors

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ABSTRACT

Toxic cyanobacterial blooms are a major issue in freshwater systems in many countries. The potentially toxic species and their ecological causes are likely to be different in tropical zones from those in temperate water bodies; however, studies on tropical toxic cyanobacterial blooms are sporadic and currently there is no global synthesis. In this review, we examined published information on tropical cyanobacterial bloom occurrence and toxin production to investigate patterns in their growth and distribution. Microcystis *was the most frequently occurring bloom genus throughout tropical Asia, Africa and Central America, while* Cylindrospermopsis *and* Anabaena *blooms occurred in various locations in tropical Australia, America and Africa.* Microcystis *blooms were more prevalent during the wet season while* Cylindrospermopsis *blooms were more prevalent during the dry period. Microcystin was the most encountered toxin throughout the tropics. A meta-analysis of tropical cyanobacterial blooms showed that* Microcystis *blooms were more associated with higher total nitrogen concentrations, while* Cylindrospermopsis *blooms were more associated with higher maximum temperatures. Meta-analysis also showed a positive linear relationship between levels of microcystin and N:P (nitrate:phosphate) ratio. Tropical African* Microcystis *blooms were found to have the lowest microcystin levels in relation to biomass and N:P (nitrate:phosphate) compared to tropical Asian, Australian and American blooms. There was also no significant correlation between microcystin concentration and cell concentration for tropical African blooms as opposed to tropical Asian and American blooms. Our review illustrates that some cyanobacteria and toxins are more prevalent in tropical areas. While some tropical countries have considerable information regarding toxic blooms, others have few or no reported studies.*

Key words: Cyanobacterial blooms, tropical areas, toxin production, Microcystis*,* Cylindrospermopsis*, N:P.*

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INTRODUCTION

Cyanobacterial blooms have been recognised as a health issue in freshwater systems in many countries (Briand *et al*., 2003; Falconer, 2008) mainly because some species are capable of producing potent toxins that are harmful to humans and animals. Currently there are two types of cyanotoxins that are particularly problematic to humans: hepatotoxins (cyclic peptides) and neurotoxins (alkaloids) (Sivonen, 1999; Stewart *et al*., 2008; Wiegand and Pflugmacher, 2005; Zurawell *et al*., 2005; Chen *et al*., 2009). Toxin-producing cyanobacteria have been responsible for serious cases of human and livestock poisoning and deaths in a number of countries worldwide (e.g., in Brazil, Australia and North America) (Francis, 1878; Beasley *et al*., 1989; Azevedo *et al*., 2002; Cox *et al*., 2005; Sotero-Santos *et al*., 2006).

In one of the most serious incidents in the tropics, 116 kidney dialysis patients in Northeast Brazil suffered from liver failure, resulting in 52 fatalities, due to dialysis water that was sourced from a nearby reservoir contaminated with microcystins in 1996 (Carmichael, 1996; Joachimsen *et al*., 1998; Carmichael *et al*., 2001; Komarek *et al*., 2001; Azevedo *et al*., 2002). Since that incident some studies have been carried out on several reservoirs in South and Central America documenting blooms and progenitor species (Díaz-Pardo *et al*., 1998; Carmichael *et al*., 2001; Lind and Davalos-Lind, 2002; Ramirez *et al*., 2002; Bittencourt-Oliveira *et al*., 2005; Frias *et al*., 2006; Merino-Ibarra *et al*., 2007; Berry and Lind, 2010; Vasconcelos *et al*., 2010; Rejmánková *et al*., 2011). A review by Dorr *et al*. (2010) revealed that there has been increased cyanobacterial bloom occurrence in water bodies in South America requiring better methods for screening and testing of cyanobacterial toxins.

Another case of human hepatoenteritis caused by cyanobacterial toxin poisoning in a tropical area occurred on Palm Island, Australia, in 1979, where 148 adults and children were affected by the toxin in their drinking water taken from a lake with high levels of the cyanobacterial species *Cylindrospermopsis raciborskii*, which is known to produce cylindrospermopsin, a newly identified hepa-

totoxin at that time (Hawkins *et al*., 1985). These cases illustrate the importance and need to understand the toxin producing cyanobacterial species, their prevalence and causes of blooms.

Although cyanobacterial blooms are a worldwide phenomenon, there are differences in the typical species and toxins found in temperate and tropical areas (Bartram *et al*., 1999). However, most published studies focus on cyanobacterial toxins and blooms in temperate regions with considerably less work reported from tropical areas. Nevertheless, as demonstrated by the cyanotoxin cases in Brazil and Australia, toxic cyanobacterial blooms in tropical countries can occur with considerable harmful effect. Within the tropics, cyanobacterial toxins and blooms have been more intensively studied in certain countries such as Brazil, Australia and Thailand, but an overall global review of blooms in the tropics is lacking. This review aims to address this gap by highlighting cyanobacterial bloom studies undertaken in tropical areas. In this review, data on the i) prevalence, problem taxa, toxin production and ii) influencing environmental factors for toxic cyanobacterial blooms is assessed for tropical countries across four continents. This information is synthesised and evaluated to reveal trends across tropical countries, which may be different from those in sub-tropical and temperate locations.

METHODS

The literature was located using Web of Science and Google Scholar using the keywords: *cyanobacteria*, *blooms*, *tropics* and *tropical countries*, with specific country searches for the period between 1970 and 2013. For the purpose of this review, the word *bloom* was defined as Alert Level 1 by the World Health Organization (Bartram *et al*., 1999), which denotes high biomass (cell counts of 2000 cells mL^{-1} or 0.2 mm^3 L^{-1} biovolume or 1 µg L^{-1} chlorophyll *a*) of cyanobacterial species in a water body. In total, 142 papers covering 186 water bodies were obtained from regional and international journals for the qualitative discussion of overall trends in cyanobacterial blooms. Percentages of dominant cyanobacterial bloom genera were calculated for all the tropical blooms reported. A subset of 66 papers covering 91 water bodies was chosen based on information on cyanobacteria toxins found, for example, microcystins (MC-RR & MC-LR) were found via LC-MS testing. These papers were used to calculate percentage of different cyanobacterial toxins detected for the toxic tropical cyanobacterial blooms reported.

A subset of 33 papers covering 48 water bodies was selected for a meta-analysis of environmental factors influencing bloom formation. The criterion for choosing these 33 studies was availability of data on the identification of the bloom species, highest total nitrogen concentration (TN, mg L^{-1}), highest total phosphorus concentration (TP, mg L^{-1}), and minimum and maximum temperatures. In order to ascertain which factors were more important for tropical bloom formation, metadata on environmental variables and genera of cyanobacteria were examined for relationships using non-metric multidimensional scaling (NMDS) (R, Vegan package, Oksanen *et al*., 2013). Blooms were arranged by presence or absence of dominant genera (*Microcystis*, *Cylindrospermopsis*, *Anabaena,* and *Planktothrix*). An NMDS was run on the genera data, which contained 48 data points from tropical Asia, America, Australia and Africa. As cyanobacterial biomass was not recorded by all of the 33 studies it was not used as a criterion for the meta-analysis. The environmental variables (highest total nitrogen concentration, highest total phosphorus concentration, total nitrogen to total phosphorus ratio based on molar ratios, minimum and maximum temperatures) were then fitted onto the NMDS using envfit (R, Vegan package, Oksanen *et al*., 2013). To analyse the effect of types of water bodies on cyanobacterial bloom genera present, the meta-data created above was analysed using NMDS and Adonis (Permutational Multivariate Analysis of Variance using Distance Matrices) and plotted using ordiellipse (R, Vegan package, Oksanen *et al*., 2013).

In order to analyse the relationship between nutrient levels and microcystin levels, eight papers covering 14 water bodies were selected based on the availability of information for i) maximum total microcystin concentration (µg L^{-1}); ii) nitrate (mg L^{-1}) in the water body at the time of the maximum microcystin concentration; iii) phosphate (orthophosphate/soluble reactive phosphorous, PO_4) (mg L^{-1}) in the water body at the time of the maximum microcystin concentration. A regression analysis on nitrate, phosphate, N:P (nitrate: phosphate), and maximum total microcystin concentration was then carried out using Spearman's correlation coefficient (rho). For the analysis of maximum temperatures and microcystin concentration, 11 papers covering 17 water bodies were selected based on the availability of information on i) maximum (highest) temperatures of water body during sampling and ii) maximum total microcystin concentration (µg L^{-1}). A regression analysis on the maximum temperature of the water body and the maximum total microcystin concentration was carried out using Spearman's correlation coefficient (rho). For the analysis of *Microcystis* biomass and microcystin concentration, eight papers covering 27 water bodies were selected based on availability of information: i) total microcystin concentration (µg L^{-1}); ii) cell count of *Microcystis* from the same water body. A regression analysis on the *Microcystis* cell count and microcystin concentration was then carried out using Spearman's correlation coefficient (rho).

RESULTS AND DISCUSSION

Prevalence, problem taxa, toxin production

General patterns of cyanobacteria and cyanotoxins across tropical areas

Microcystis was the most prevalent bloom-causing genus in tropical Africa and Asia, while *Cylindrospermopsis* was the most common in tropical Australia and the second most prevalent genus in tropical Asia (Fig. 1). *Microcystis* and *Cylindrospermopsis* blooms have occurred in similar frequency in tropical America. *Anabaena* blooms were the second most frequently occurring genus in tropical Africa. As expected, the frequency of cyanobacterial bloom occurrence in tropical Australia was much lower compared to that of other tropical countries, due to the relatively smaller land area of tropical northern Australia.

The most frequently encountered toxin throughout the tropics was microcystin except for tropical Australia where cylindrospermopsin was more frequently encountered (Fig. 2). The frequent occurrence of cylindrospermopsin in Australia was expected given the higher frequency of recorded *Cylindrospermopsis* blooms (Griffiths and Saker, 2003). The second most encountered toxin in Africa was anatoxin, produced by blooms of *Anabaenopsis*, *Arthrospira* and *Anabaena* species (Ballot *et al*., 2005; Odokuma and Isirima, 2007). Despite the presence of *Anabaena* in tropical Asia, anatoxin was not detected, with the only two toxins detected being microcystin and cylindrospermopsin. The lack of expertise required for testing for neurotoxins may partly account for the lack of documented occurrences (Jewel *et al*., 2003).

Saxitoxin was detected in tropical American and tropical African blooms by HPLC and various other detection methods (ESI, LC-MS, FLD). This toxin was produced by blooms of *Cylindrospermopsis* and *Lyngbya* in Brazil, Mexico, Guatemala and Nigeria (Lagos *et al*., 1999; Bouvy *et al*., 1999; Molica *et al*., 2005; dos Anjos *et al*., 2006; Berry and Lind, 2010; Rejmánková *et al*., 2011; Sant'Anna *et al*., 2011). Comparisons of the neurotoxic *Cylindrospermopsis* strains from Brazil and Mexico revealed the Brazilian strain to have acute neurotoxicity from the presence of saxitoxin, neosaxitoxin and decarbamoylsaxitoxin and the Mexican strains isolated were found to be non-toxic (Bernard *et al*., 2003).

Patterns in toxin testing across the tropics

The percentage of cyanobacterial blooms that undergo toxin testing has increased in tropical Africa and America and remained relatively constant in tropical Australia from the 1990s to the present, but decreased in tropical Asia. Many blooms that occur in tropical Asia are not tested for toxins despite reports of fish kills or harm to livestock (Tab. 1); this could be due to a lack of expertise and cyanotoxin testing equipment (Jewel *et al*., 2003). Another reason could be a greater focus on the general limnology of lake ecosystems rather than cyanobacterial bloom formation or its management (Mizuno and Mori, 1970; Lewis 1973, 1978; Green *et al*., 1976, 1978). Toxin testing in India, Bangladesh, Philippines, Singapore, Sri Lanka, Thailand, and Vietnam have been carried out using HPLC (high performance liquid chromatography) and various detection methods from UV (ultraviolet) to MALDI-TOF (matrix assisted laser desorption time of flight mass spectrometry) (Tab. 1). Blooms in Australian water bodies were tested using mouse bioassays in the 1990s, and later by HPLC for more detailed toxin results (Saker and Griffiths, 2001; Griffiths and Saker, 2003; White *et al*., 2003; Bor-

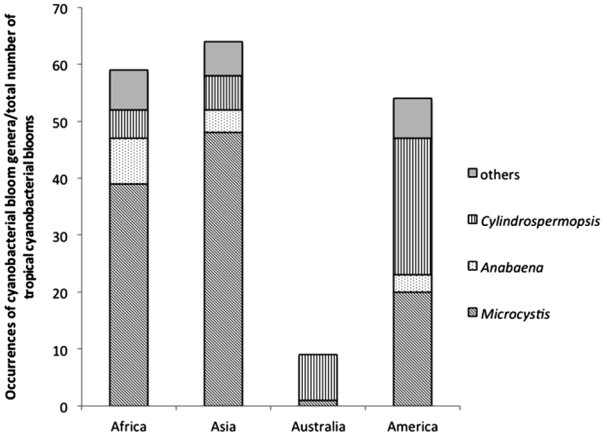

Fig. 1. Proportion of tropical cyanobacterial genera, out of total number of tropical cyanobacterial blooms.

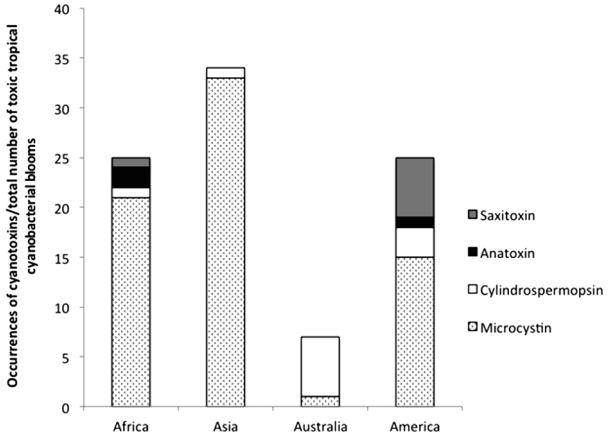

Fig. 2. Proportion of different cyanobacterial toxins, out of total number of toxic tropical cyanobacterial blooms.

mans *et al*., 2004). In the case of tropical Africa, many of the blooms were detected in reservoirs and lakes used for drinking water, highlighting a need for toxicity testing in these countries (Akin-Oriola *et al*., 2006). Past studies of bloom occurrence and toxin testing via ELISA test kits/HPLC and MALDI-TOF MS have been carried out in Ethiopia, Ghana, Nigeria, Uganda, Kenya, Tanzania and Zimbabwe but few or no studies in other central African countries, such as The Democratic Republic of Congo, Central African Republic and South Sudan (Tab. 2, Fig. 3).

An increase in toxin testing in tropical America was most prominently seen in Brazil, Mexico and Guatemala

Tab. 1. Summary of cyanobacterial blooms, prevalence and toxins recorded in tropical Asia and Australia.

Country	Potential toxic species found	Toxin test	Toxins found	Amount of toxins	References
Australia	*Cylindrospermopsis raciborskii*, Aphanizomenon* sp.*, Anabaena* sp.*, Anabaena tenericaulis* & *Microcystis panniformis**	Mouse bioassay & HPLC/MS	CYN & MC	CYN: 1.0-20 µg/L, MC: 1000-2500 µg/L	Hawkins *et al*., 1985; Hawkins and Griffiths, 1993; McGregor and Fabbro, 2000; Saker and Griffiths, 2001; Griffiths and Saker, 2003; White *et al*., 2003; Bormans *et al*., 2004
Bangladesh	*Microcystis aeruginosa*, Microcystis* sp.**, Anabaena flos-aquae* & *Planktothrix* sp.	RP-HPLC & HPLC/LCMS & HPLC/UV	MC-LR,-RR,-YR	0.14-1360 µg/L	Welker *et al.*, 2004; Ahmed *et al.*, 2008; Ahmed and Luckas, 2008; Jahan *et al.*, 2010
Cambodia	*Microcystis aeruginosa*	Not tested	Not tested	Not tested	Campbell *et al*., 2006
Hong Kong	*Microcystis aeruginosa, M. Incerta* & *Anabaena flos-aquae*	Not tested	Not tested	Not tested	Hodgkiss, 1974
India	*Microcystis aeruginosa*, M. novacekii, M. viridis*, M. wesenbergii* & *M. icthyoblabe*	RP-HPLC/ MALDI-TOF & RP-HPLC/ LC/ESI/MS	MC-LR,-RR	280-1540 µg/g	Agrawal *et al*., 2006; Tyagi *et al*., 2006; Prakash *et al*., 2009; Sangolkar *et al*., 2009
Indonesia	*Microcystis aeruginosa, Cylindrospermopsis raciborskii* & *Planktothrix agardhii*	Not tested	Not tested	Not tested	Padisak (1997); Prihantini *et al.*, (2008); Retnaningdyah *et al.*, (2010)
Malaysia	*Microcystis* spp., *Cylindrospermopsis raciborskii* & *Planktothrix agardhii*	Not tested	Not tested	Not tested	Rouf *et al*., (2008); Harith and Hassan (2011); Mansoor *et al*., (2011)
Myanmar	*Microcystis* spp.	Not tested	Not tested	Not tested	Green (2010)
Philippines	*Microcystis aeruginosa*, Cylindrospermopsis raciborskii*	HPLC/ MALDI-TOF	MC-LR	11472-12158 µg/g	Cuvin-Aralar *et al*., (2002); Baldia *et al*., (2003); Baldia *et al*., (2007)
Singapore	*Microcystis* spp.**, Cylindrospermopsis raciborskii, Planktothrix* sp. *Anabaena* sp. & *Aphanizomenon* sp.	HPLC/LC–MS	MC-LR	2660-2800 µg/L	Yang and Chiam-Tai (1991); Sim (2009); Te and Gin (2011)
Sri Lanka	*Microcystis aeruginosa*, M.incerta*, Anabaena* sp. & *Planktothrix* sp.	HPLC/ET-MS	MC-LR,-RR	0.8-81 µg/L	Jayatissa *et al*., (2006)
Thailand	*Microcystis aeruginosa*, M. wesenbergii* & *Cylindrospermopsis raciborskii**	ELISA/HPLC-MS	MC-LR,-RR,-YR, CYN	MC: 2.2±3.0 µg/L and 9.4±2.0 µg/L CYN: 1020 µg/g	Mahakhant *et al.*, (1998); Li *et al.*, (2001); Wang *et al.*, (2002); Prommana *et al.*, (2006); Khuantrairong *et al.*, (2008)
Vietnam	*Microcystis* spp.*, Jaaginema* sp.*, Arthrospira masartii, Oscillatoria perornata, Planktothrix zahidii* & *Pseudanabaena cf. moniliformis**	ELISA/HPLC-UV	MC-LR,-RR	2.94 µg/L and 18.94 µg/L	Nguyen *et al*., (2007a); Nguyen *et al*., (2007b); Dao *et al*., (2010)

*MC, Microcystin; CYN, Cylindrospermopsin; *species tested for toxins.*

with testing carried out via mouse and fish bioassay, ELISA & HPLC/PDA, MALDI-TOF (Tab. 3). This increase was probably motivated by the two incidents that led to human fatalities in 1988 and 1996 (Teixeira *et al*., 1993; Domingos *et al*., 1999; Carmichael *et al*., 2001; Azevedo *et al*., 2002; Molica 2002). Few studies have been conducted in other countries such as Panama and Colombia (Bartram *et al*., 1999; Dorr *et al*., 2010).

Problem taxa - Prevalence in tropical water bodies and toxins produced

Microcystis

Tropical Asia and Australia

The majority of blooms (77%) in tropical Asia were caused by *Microcystis* spp., usually *Microcystis aeruginosa* (Fig. 1; Tab. 1). Several species (*M. aeruginosa*, *M. no-*

Tab. 2. Summary of cyanobacterial blooms, prevalence and toxins recorded in tropical Africa.

Country	Potential toxic species found	Toxin test	Toxins found	Amount of toxins	References
Cameroon	*Planktothrix mougeotii*, *Oscillatoria putrida* & *Microcystis* spp. *(M.aeruginosa, M. wesenbergii)*	Not tested	Not tested	Not tested	Kemka *et al*., 2003; Green, 2010
Cote d'lvoire	Unknown bloom-forming species	Not tested	Not tested	Not tested	Bouvy *et al*., (1998); Arfi *et al*., (2001)
Ethiopia	*Microcystis* sp.*	ELISA	No MC found	No MC found	Gremberghe *et al*., (2011)
Ghana	*Microcystis aeruginosa** & *Anabaena flos-aquae*	HPLC	MC-RR	0.03-3.21 µg/L	Addico *et al*., (2006)
Kenya	*Microcystis aeruginosa**, *Arthrospira fusiformis** & *Anabaenopsis abijatae**	ELISA/HPLC-MALDI-TOF	MS MC-LR & Anatoxin-a	MC: 1.6-39.0 µg/g Anatoxin: 0.5-2.0 µg/g	Ballot *et al*., (2005); Haande *et al*., (2007); Kotut *et al*., (2010)
Malawi	*Anabaena* sp.	Not tested	Not tested	Not tested	Gondwe *et al*., (2007)
Nigeria	*Cylindrospemopsis* sp*. *Anabaena* sp.*, *Microcystis* sp.* *(Microcystis aeruginosa, M. flos-aquae, M. wesenbergii), Lyngbya* sp.*, *Aphanizomenon flos-aquae, Oscillatoria limnetica & Anabaena spiroides*	ELISA/ HPLC-MALDI-TOF	MC, CYN, Anatoxin-a, Anatoxin-a(s), STX	MC: 1.4-3.8 µg/L	Anadu *et al*., (1990); Kemdirim (2000); Ezra and Nwankwo (2001); Akin-Oriola (2003); Akin-Oriola *et al*., (2006); Odokuma and Isirima (2007); Chia *et al*., (2009); Okechukwu and Ugwumba (2009); Onyema (2010); Ajuzie (2012)
Senegal	*Microcystis aeruginosa & Cylindrospermopsis raciborskii*	Mouse bioassay	No CYN/STX found	No CYN/STX found	Berger *et al*., (2006); Bouvy *et al*., (2006); Dufour *et al*., (2006)
Tanzania	*Anabaena* sp., *Microcystis* sp.*	HPLC-DAD/ MALDI-TOF	MC-RR	0-1.0 µg/L	Sekadende *et al*., (2005)
Uganda	*Microcystis aeruginosa, M. flos-aquae, Anabaenopsis* spp., *Aphanizomenon* sp., *Anabaena* sp. *& Cylindrospermopsis raciborskii*	ELISA, HPLC/MALDI-TOF & LC-MS/MS	MC-RR, (Asp3) MC-RR, MC-YR, (Asp3) MC-YR,MC-LR, MC-RY, (Asp3) MC-RY	0.2–61.2 µg/L	Ganf (1974); Komarek and Kling (1991); Oliver and Ganf (2000); Haande *et al*., 2007); Haande *et al*.,(2008); (Green (2010); Okello *et al*., (2010); Okello & Kurmayer (2011); Poste *et al*., (2013)
Zimbabwe	*Microcystis aeruginosa**, *M. wesenbergii, M. novacekii, C. raciborskii, Lyngbya* sp., *Anabaena* sp., *Aphanizomenon* sp. *& Oscillatoria* sp.	ELISA	MC-LR	0.2–22.48 µg/L	Ramberg (1987); Magadza (2006); Mhlanga *et al*., (2006a); Mhlanga *et al*., (2006b); Magadza (2008–2009); Kunz (2011); Tendaupenyu (2012); Mhlanga (n.d.)

*MC, Microcystin; CYN, Cylindrospermopsin; *species tested for toxins.*

vacekii, *M. viridis*, *M. wesenbergii* and *M. ichthyoblabe*) occurred as blooms in different countries and samples containing *M. aeruginosa*, *M. viridis* and *M. incerta* (now *Aphanocapsa incerta*) produced microcystins (microcystin LR, RR and YR) (Tab. 1). In Asia, 66% of *Microcystis* blooms produced microcystins; the remaining blooms in Myanmar and Indonesia were not tested for toxins (Fig. 4, Tab. 1). Evidence from Myanmar and Indonesia were based on papers that lacked taxonomic detail and toxin analysis (Tab.1). Therefore, the cyanobacterial bloom occurrences from these countries are likely to be an underestimate of actual cyanobacterial bloom occurrences.

Microcystis blooms in Bangladesh, Sri Lanka, Vietnam, Thailand, Singapore and the Philippines have recorded microcystin levels above the WHO drinking water guideline level of 1 μg L^{-1} (Cuvin-Aralar *et al*., 2002; Wang *et al*., 2002; Baldia *et al*., 2003; Welker *et al*., 2004; Jayatissa *et al*., 2006; Prommana *et al*., 2006; Nguyen *et al*., 2007b). In India, livestock poisoning as well as skin lesions in children were reported from the shores of lakes and reservoirs (Agrawal *et al*., 2006). A bloom in Bangladesh may have resulted in massive fish kills and reduction in livelihood of the communities that depend on fishing for subsistence (Jewel *et al*., 2003); however, no toxin analysis was carried out on the bloom and fish samples (Jewel *et al*., 2003). Other studies on *Microcystis* blooms in Bangladesh by the World Health Organization (Welker *et al*., 2004) confirm the presence of microcystins in the drinking water bodies.

There was only one notable *Microcystis* bloom in trop-

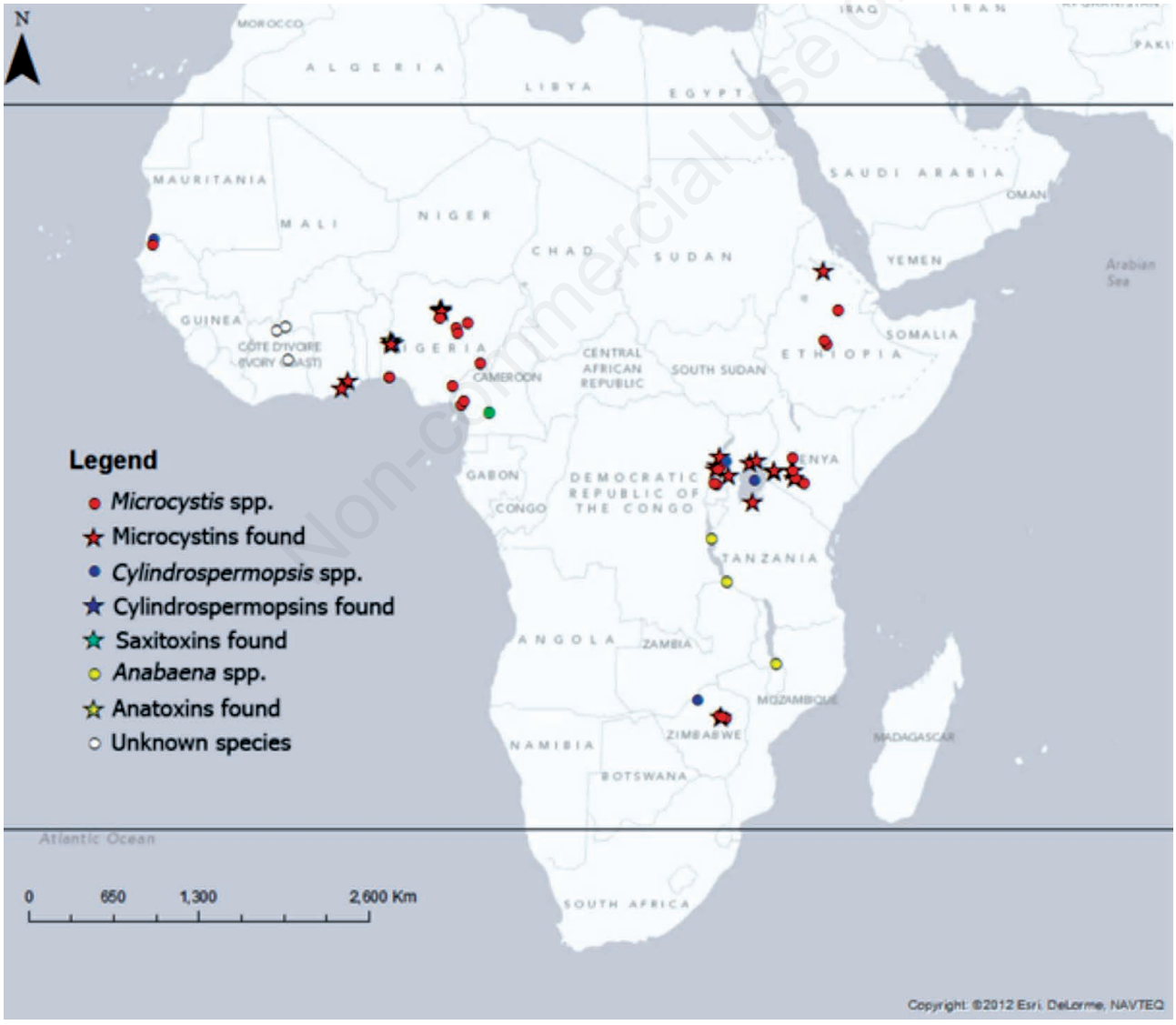

Fig. 3. Map of tropical Africa showing locations of cyanobacterial blooms, horizontal lines enclose the tropical region around the equator.

ical Australia, recorded from Lake Elphinstone, caused by *Microcystis panniformis,* with a very high microcystin level of 2500 µg L^{-1} (White *et al*., 2003). It is notable that *M. panniformis* was not found to produce high levels of toxins in tropical Asia (Tab. 1) although it formed a bloom with extremely high toxin levels in tropical Australia.

Tropical Africa

Microcystis was the bloom-causing genus in 66% of blooms in tropical African countries (Figs. 1 and 3; Tab. 2). The main species responsible were *M. aeruginosa, M. flos-aquae* and *M. wesenbergii,* which produced microcystins (MC–RR, (Asp3) MC–RR, MC–YR, (Asp3) MC–YR, MC–LR, MC–RY, (Asp3) MC–RY) in Ethiopia, Ghana, Tanzania, Nigeria, Uganda and Zimbabwe (Tab. 2). Of these countries, microcystin levels higher than 1 µg L^{-1} were recorded from water bodies in Ghana, Nigeria, Uganda and Zimbabwe (Ndebele and Mhlanga, 2006; Chia *et al*., 2009; Kotut *et al*., 2010; Sitoki *et al*., 2012). The highest microcystin level of 61.2 µg L^{-1} was detected in a cyanobacterial bloom in Lake Saka, Uganda (Okello *et al*., 2010; Okello and Kurmayer, 2011, Poste *et al*., 2013). Little is known about toxin production by *Microcystis* blooms in Cameroon and Senegal as they have not been tested (Tab. 2).

Tropical America

In tropical America, 35% of total blooms were caused by species of *Microcystis*, namely *M. aeruginosa, M. panniformis, M. protocystis, M. novacekii* and *M. viridis* (Figs. 1 and 5; Tab. 3), with concentrations of microcystins above

Tab. 3. Summary of cyanobacterial blooms, prevalence and toxins recorded in tropical America.

Country	Potential toxic species found	Toxin test	Toxins found	Amount of toxins	References
Brazil	*Cylindrospermopsis raciborskii*, Microcystis aeruginosa*, M. novacekii*, M. panniformis*, M. protocystis*, M. viridis*, Planktothrix agardhii*, Aphanizomenon* sp., *Oscillatoria* sp., *Anabaena oumiana, A. crassa; Dolichospermum circinalis (formerly Anabaena circinalis)* & *Radiocystis fernandoi**	Mouse and fish bioassay, ELISA & HPLC/PDA, MALDI-TOF MC-RR, MC-hRhR,	MC-LR,MC-YR, CYN, STX, NEO, GTX1,GTX2, GTX3, GTX4, Anatoxin-a(s)	MC-LR: 19.5 µg/L STX: 9.3 MU/mg dry cells	Branco and Senna (1994); Bouvy *et al*., (1999); Domingos *et al*., (1999); Bouvy *et al*., (2000); Huszar *et al*., (2000); Carmichael *et al*., (2001); Azevedo *et al*., (2002); Molica (2002); Bittencourt-Oliveira (2003); Vieira *et al*., (2003); Vieira *et al*., (2005); dos Anjos *et al*., (2006); Frias *et al*., (2006); Sotero-Santos *et al*., (2006); Sant'Anna *et al*., (2007); Sant'Anna *et al*., (2008); Figueredo and Giani (2009); Werner and Laughinghouse IV (2009); Molica *et al*., (2005); Bouvy *et al*., (2003); Bittencourt-Oliveira *et al*., (2011); Moura *et al*., (2007); Ferrão-Filho *et al*., (2007); Piccin-Santos & Bittencourt, (2012); Soares *et al*., (2012)
Guatemala	*Lyngbya hieronymusii*, L. birgei*, & L. robusta**	LC-MS/MS	CYN & STX	CYN: 0.6-1.2 ng/L, STX: 2.9-5.8 ng/L	Rejmánková *et al.*, 2011
Mexico	*Microcystis aeruginosa*, M. panniformis*, M. protocystis*, Planktothrix agardhii*, Cylindrospermopsis catemaco*, C. philippinensis*, Pseudanabaena mucicola, Anabaena* sp., *Nostoc* sp. & *Oscillatoria* sp.	ELISA/HPLC/ LC-MS/MALDI-TOF	MC-LR,-FR, HYR, YR, HtYR, CYN & STX	MC: 4.9 µg/L-78 µg/L, CYN: 21.34±2.00 ng/L, STX: 5.30±2.56 ng/L	Díaz-Pardo *et al*., (1998); Lind and Davalos-Lind (2002); Ramirez *et al*., (2002); Romero (2002) Merino-Ibarra *et al*., (2007); Berry and Lind (2010); Vasconcelos *et al*., (2010)
Venezuela	*Microcystis aeruginosa, Anabaena volzii, A. spiroides* & *Anabaenopsis* sp.	Not tested	Not tested	Not tested	Lewis (1986)

*MC, Microcystin; CYN, Cylindrospermopsin; *species tested for toxins.*

1 µg L^{-1} recorded from lake and reservoir water in Mexico and Brazil (Tab. 3). Microcystins were also detected from *Radiocystis fernandoi* in Brazil (Vieira *et al*., 2003), a species that did not produce toxins in tropical Asia, Australia or Africa. The greatest number of microcystin variants (MC-LR, FR, HYR, YR, HtYR) was detected from water bodies in Mexico (Tab. 3). Although *Microcystis aeruginosa* was detected in Venezuela, it was not tested for toxins and thus, little is known about occurrences of microcystins in this country (Tab. 3). A study in Sao Paulo, Brazil, found that *Microcystis* strains could produce paralytic shellfish poisons or PSPs, namely GTX4 (47.6%), GTX2 (29.5%), GTX1 (21.9%), GTX3 (1.0%) as well as a microcystin (MC-RR) (Sant-Anna *et al*., 2011). The production of neurotoxins by *Microcystis* has never been recorded in any of the other tropical blooms.

Cylindrospermopsis

Tropical Asia and Australia

The second most prevalent genus in tropical Asia was *Cylindrospermopsis* (Figs. 1 and 4). This genus was encountered in six out of thirteen countries in tropical Asia (Tab. 1). The genus was bloom-forming in Singapore and potentially so in Thailand and Vietnam (Khoo *et al*., 1977; Li *et al*., 2001; Pongswat *et al*., 2004; Meesukko *et al*., 2007; Khuantrairong and Traichaiyaporn, 2008; Dao *et al*., 2010). The only bloom-forming species was *Cylin-*

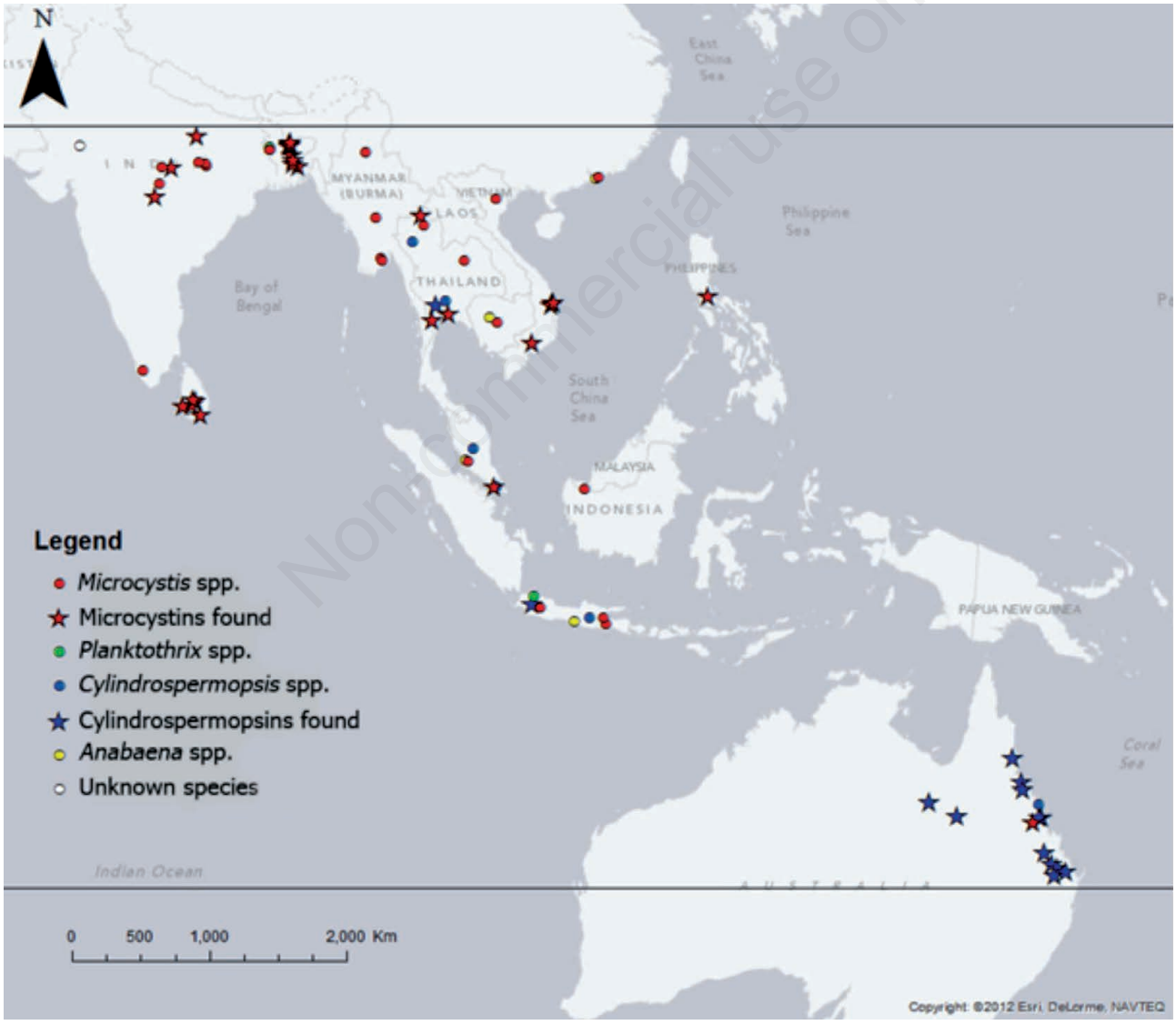

Fig. 4. Map of tropical Asia and Australia showing locations of cyanobacterial blooms, horizontal lines enclose the tropical region around the equator.

drospermopsis raciborskii, although recent taxonomic revisions now recognise more than one species, *e.g*., coiled morphotypes of *C. raciborskii* are now known as *C. philippinensis* (Komárek and Mareš, 2011). Even though *C. raciborskii* has been bloom-forming in one country and commonly found in two others, cylindrospermopsin production of 1.02 mg g^{-1} was recorded from only one study in Thailand (Li *et al*., 2001). The toxin level of this strain was much lower than an Australian strain cultured in the same conditions (1.358 mg g^{-1}) (Li *et al*., 2001).

In contrast to tropical Asia, *Cylindrospermopsis* was the dominant bloom-forming genus in tropical Australia, accounting for seven out of eight blooms (Figs. 1 and 4; Tab. 1). *C. raciborskii* blooms from Palm Island were highly toxic with cylindrospermopsin levels of up to 20 µg L^{-1} recorded (McGregor and Fabbro, 2000; Griffiths and Saker, 2003). Additionally, *C. raciborskii* blooms from Palm Island were strongly implicated in the severe hepatoenteritis poisoning of 149 people in 1979 (Hawkins *et al*., 1985).

Tropical Africa

Cylindrospermopsis blooms were the second most prevalent blooms in tropical Africa (Fig. 1). It was found in four out of eleven countries including Nigeria, Senegal, Uganda and Zimbabwe (Tab. 2; Fig. 3). The only species recorded was *Cylindrospermopsis raciborskii*; however, only strains from ponds in Nigeria were found to produce cylindrospermopsin (Odokuma and Isirima, 2007). Strains from Kazinga Channel, Uganda and Lake Guiers, Senegal were isolated and tested for toxins by LC-MS and mouse bioassay respectively, but were not found to produce any cylindrospermopsin and saxitoxins (Lake Guier isolates) (Haande *et al*., 2008; Berger *et al*., 2006).

Tropical America

Cylindrospermopsis was the most encountered bloom genus in the tropical Americas occurring in 47% of all documented cyanobacterial blooms (Figs. 1 and 5). Three species were frequently encountered, *C. raciborskii*, *C. catemaco* and *C. philippinensis* (Tab. 3). These blooms were recorded from Brazil and Mexico (Fig. 5; Tab. 3). Saxitoxins (STX, NEO, GTX2 and GTX3) and cylindrospermopsins were produced by several strains of *Cylindrospermopsis* isolated from Brazil and Mexico (Bouvy *et al*., 1999; Molica *et al*., 2002; Molica *et al*., 2005; dos Anjos *et al*., 2006; Frias *et al*., 2006; Ferrão-Filho *et al*., 2007; Berry and Lind, 2010). The *Cylindrospermopsis* blooms in the tropical Americas differ from the *Cylindrospermopsis* strains isolated in Thailand and Australia, in that they produced saxitoxin in addition to cylindrospermopsins (Tabs. 1, 2 and 3).

Other problem taxa

Anabaena

Less than 7% of total blooms that occurred in tropical Asia were dominated by *Anabaena* spp. (Tab. 1, Fig. 4). These blooms were not tested for toxins, although a bloom of *Anabaena flos-aquae* in Bangladesh caused massive fish kills (Jewel *et al*., 2003). *Anabaena* blooms also occurred in Nigeria, Tanzania, Ghana, and Malawi (Tab. 2; Fig. 3). Microcystin variants were detected in raw water in Ghana containing *A. flos-aquae* and *Microcystis aeruginosa*, thus, toxin production could not be attributed specifically to *A. flos-aquae* (Addico *et al*., 2006). The only *Anabaena* sp. blooms that tested positive for anatoxin-a and anatoxin-a(s) occurred in Nigeria (Odokuma and Isirima 2007). In Tapacura Reservoir in Brazil, blooms of *Anabaena spiroides* co-dominated with *Cylindrospermopsis raciborskii*. *Anabaena spiroides* was found to produce anatoxin-a(s) and a mixed bloom sample of *C. raciborskii* and *A. spiroides* was found to contain saxitoxins (Stx and NeoStx) (Molica *et al*., 2005).

Planktothrix

Planktothrix blooms were found in four out of thirteen tropical Asian countries including Malaysia, Indonesia, Vietnam, Singapore and Thailand (Li *et al*., 2001; Merican *et al*., 2006; Nguyen *et al*., 2007b; Prihantini *et al*., 2008; Pham *et al*., 2011). *Planktothrix agardhii,* a possible toxin producing species, is currently known to form blooms in Indonesia and Brazil (Akcaalan *et al*., 2006; Moura *et al*., 2011). *P. agardhii* blooms in Carpina Reservoir, Brazil were found to co-dominate with *C. raciborskii*. These blooms were not tested for toxins, although some strains of *P. agardhii* can produce hepatotoxins (Janse *et al*., 2005).

Planktothrix zahidii was bloom-forming in Vietnam (Nguyen *et al*., 2007a). However, this species did not produce any microcystins. Toxin testing on other *Planktothrix* species in Malaysia, Indonesia, Singapore and Thailand has yet to be reported.

Pseudanabaena

While microcystins are mostly produced by *Microcystis* spp., one microcystin variant (MC-LR) was also produced by a strain of *Pseudanabaena* cf. *moniliformis* isolated in Vietnam (Tab. 1). This species was detected in lower concentrations in the reservoirs compared with *Microcystis* spp. Another species, *Pseudanabaena mucicola,* was also recorded in water bodies in Mexico and Brazil and *Pseudanabaena* sp. was recorded in Bangladesh (Welker *et al*., 2004; Frias *et al*., 2006; Vasconcelos *et al*., 2010). Toxin testing was carried out on water bodies in all three countries containing *P. mucicola* and *Pseudanabaena* sp., but the microcystin level could not be attributed to either species due to the presence of *Microcystis*

spp. It is important to note that *Pseudanabaena* is similar in morphology to *Cylindrospermopsis*, thus, records of *Pseudanabaena* in Mexico, Brazil and Bangladesh (Welker *et al*., 2004; Frias *et al*., 2006; Vasconcelos *et al*., 2010), which did not include pictures and formal descriptions of *Pseudanabaena* species could not be verified, and might potentially be misidentifications.

Arthrospira *and* Anabaenopsis

Blooms of *Arthrospira fusiformis* and *Anabaenopsis abijitae* that produced anatoxin-a were recorded in the Kenyan rift lakes (Ballot *et al*., 2005; Odokuma and Isirima, 2007) (Tab. 2; Fig. 3). These species were otherwise not bloom-forming in any other tropical country.

Lyngbya

Lyngbya spp. blooms were recorded in Guatemala and Nigeria, with the species from Guatemala (*L. hieronymusii, L. birgei,* and *L. robusta*) producing saxitoxins and cylindrospermopsins and the species from Nigeria (*Lyngbya* sp.) producing only saxitoxins (Odokuma and Isirima, 2007; Rejmánková *et al*., 2011). These bloom-forming species were rare or absent in other tropical regions. The levels of cylindrospermopsin and saxitoxin recorded from Guatemala were relatively low (CYN: 0.6 to 1.2 ng l^{-1}, STX: 2.9 to 5.8 ng L^{-1}) and thus, do not appear to pose an immediate danger in water supplies. However, these blooms should be monitored for any changes in toxin production level (Rejmánková *et al*., 2011). The level of saxitoxins in blooms of *Lyngbya* sp. from the Sombreiro River in Nigeria was not quantified, and thus, warrants further testing to ascertain the level of saxitoxins present (Odokuma and Isirima, 2007).

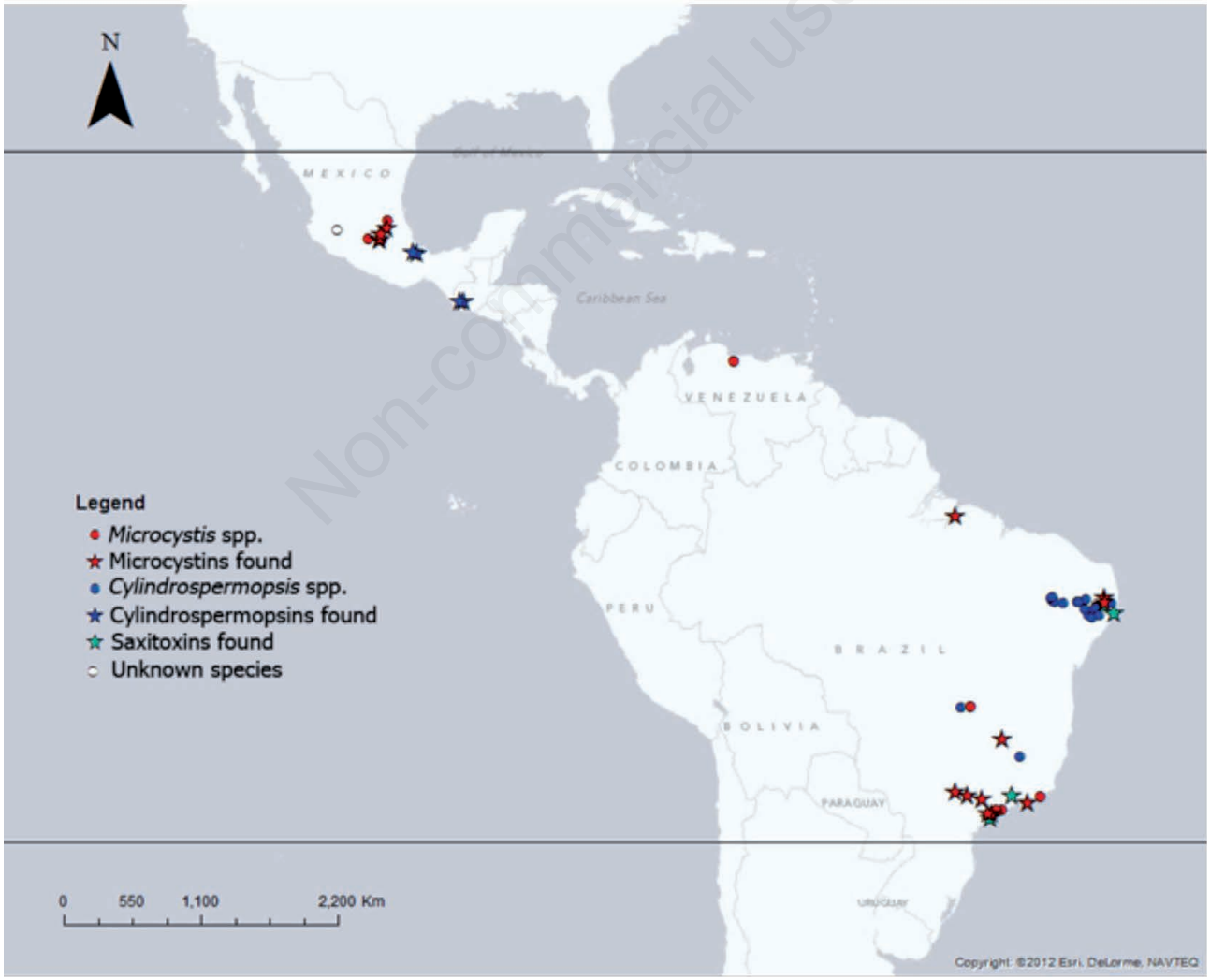

Fig. 5. Map of tropical America showing locations of cyanobacterial blooms, horizontal lines enclose the tropical region around the equator.

INFLUENCING ENVIRONMENTAL FACTORS FOR TOXIC CYANOBACTERIAL BLOOMS

Many factors contribute to the occurrence of cyanobacterial blooms. Most cyanobacterial blooms in temperate regions occur in the summer when temperature, light and nutrient conditions are suitable for cyanobacterial dominance over other species in a lake phytoplankton community (Jöhnk *et al*., 2008; Davis *et al*., 2009). This predictability of cyanobacterial blooms in temperate regions allows preventive measures to be implemented to reduce their occurrence in water bodies used for potable purposes (Mitrovic *et al*., 2011). Tropical cyanobacterial blooms tend to be affected by temperature, nutrient input, and brief periods of drought and heavy rain (Bouvy *et al*., 2000; Baldia *et al*., 2003). Unlike temperate bloom events that occur in the warmer months and last for the entirety of the summer, tropical bloom events can occur at any time of the year and usually last for a few weeks at a time (Huszar *et al*., 2000; Figueredo and Giani, 2009; Prakash *et al*., 2009).

Seasonality in the tropics

Some water bodies in the tropics encounter a distinct seasonality in wet and dry periods, with some dry periods lasting several months (Figueredo and Giani, 2009). Nitrogen-fixing species were found to be bloom-forming during the dry season, due to strong thermal stratification and water column stability (Sprober *et al*., 2003). Since nitrogen fixing genera such as *Anabaena* and *Cylindrospermopsis* are able to fix atmospheric nitrogen for growth, these genera are able to compete in conditions of lower nitrogen,

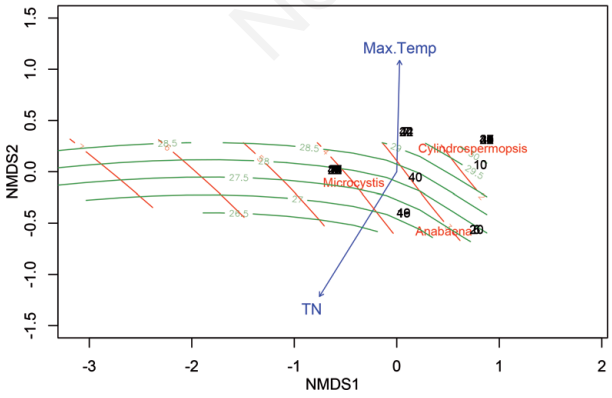

Fig. 6. Non-metric multidimensional scaling of tropical cyanobacterial blooms overlayed with maximum nitrogen levels and maximum temperatures (stress<0.01), arrows indicate nitrogen and temperature effects on bloom genera. Oblique lines represent smoothers connecting total nitrogen concentrations and green lines represent smoothers connecting maximum temperature values.

for example, after a long period of stratification (Khuantrairong *et al*., 2008; Bormans *et al*., 2004; Hawkins and Griffiths, 1993; Hawkins, 1985; Saker and Griffith, 2001; Komarek and Kling, 1991; Okechukwu and Ugwumba, 2008; Berger *et al*., 2006; Dufour *et al*., 2006; Gondwe *et al*., 2007; Branco and Senna, 1994; Bouvy *et al*., 1999; Bouvy *et al*., 2003; Vieira *et al*., 2005; Vieira *et al*., 2003). Some studies documented *Microcystis* blooms in the wet season due to elevated nutrient levels in the various water bodies, occurring after periods of heavy rainfall (Ochumba and Kibaara, 1989; Makahant *et al*., 1998; Salonen *et al*., 1999; Arfi *et al*., 2001; Kitaka *et al*., 2002; Wang *et al*., 2002; Welker *et al*., 2004; Sekandende *et al*., 2005; Meesuko *et al*., 2007; Krishnan, 2008; Onyema 2010; Sitoki *et al*., 2012). Although wet/dry seasonality in the tropics can contribute to cyanobacterial blooms, some water bodies with distinct dry and wet seasons do not show seasonality in cyanobacterial bloom occurrence (Figueredo and Giani, 2009; Werner and Laughinghouse, 2009; Frias *et al*., 2006; dos Anjos *et al*., 2006).

Effects of nutrients and temperature on tropical blooms

Based on the results of the NMDS, highest total nitrogen (TN) concentration was significantly related to the occurrences of specific cyanobacterial genera (Fig. 6) (P-value=0.025*<$P_{critical}$=0.05). Although total nitrogen was non-linearly associated with dominance of cyanobacterial genera, as seen from the surface fitting in Fig. 6, higher nitrogen levels were more associated with *Microcystis* blooms, while lower nitrogen levels were associated with *Cylindrospermopsis* blooms. Maximum temperature was also significantly related to cyanobacterial genera (Fig. 6) (P-value=0.029*. <$P_{critical}$=0.05). Higher maximum temperature was more associated with *Cylindrospermopsis* blooms compared to *Microcystis* and *Anabaena* blooms (Fig. 6).

The results of this meta-analysis corroborates some findings from individual studies across all regions, which identify elevated total nitrogen concentrations as one of the more important factors in the development of tropical *Microcystis* blooms (Mahakhant *et al*., 1998; Huszar *et al*., 2000; Cuvin-Aralar *et al*., 2002; Welker *et al*., 2004; Jayatissa *et al*., 2006; Magadza, 2006; Ghosh *et al*., 2008; Chia *et al*., 2009; Rejmánková *et al*., 2011). Other factors such as high temperature do contribute to *Microcystis* bloom formation, however, the role of temperature was not as important as total nitrogen concentration (Fig. 6). Some studies have found that higher temperatures favour *Cylindrospermopsis* blooms (Bouvy *et al*., 2000; Huszar *et al*., 2000; Saker and Griffiths, 2001; Berger *et al*., 2006; Dufour *et al*., 2006; Ghosh *et al*., 2008; Figueredo and Giani, 2009), while high total nitrogen concentration may not be as important for *Cylindrospermopsis* bloom occurrence, due to the fact that *Cylindrospermopsis* are nitrogen-fixing

cyanobacterial genera (Bouvy *et al*., 1999; Rustadi *et al*., 2002; Gondwe *et al*., 2007; Khuantrairong and Traichaiyaporn, 2008). Comparing this outcome to temperate areas, *Cylindrospermopsis* blooms in France are similarly affected by high temperature (Briand *et al*., 2002). Higher temperatures were found to be a key factor in germination of akinetes (Briand *et al*., 2002). However, it is important to note that a combination of these factors, and not a single factor alone, usually leads to the development of a bloom (Paerl *et al*., 2001; Jacoby *et al*., 2003).

Highest total phosphorus concentration was found to be non-significant (P-value=0.669 $>P_{critical}$=0.05) in relation to the genera of bloom-forming cyanobacteria from the tropics in this meta-analysis. This could be due to the fact that TN:TP ratios were below 23:1 in most studies surveyed indicating non-limiting phosphorus conditions according to Guildford & Hecky (2000) and thus, the highest total phosphorus did not have any significant effect on the genera of bloom-forming cyanobacteria.

The ratios of total nitrogen:total phosphorous (TN:TP) were also found to be non-significant (P-value=0.832 $>P_{critical}$=0.05) in relation to genera of bloom-forming cyanobacteria. This surprising outcome may not necessarily be due to the reduced importance of TN:TP in determining cyanobacterial dominance, but in the lack of long-term data present in the papers selected for the analysis. In temperate lakes, low TN:TP and stable water conditions have been shown to lead to the dominance of both nitrogen and non-nitrogen-fixing cyanobacteria (Smith *et al*., 1983). However, as noted by Paerl *et al*. (2001), TN:TP ratios may have less of an effect when total nitrogen and total phosphorous are not limiting, which seems to be the case for most tropical lakes and reservoirs in the analysis.

Another factor that has been known to affect the dominance of cyanobacterial bloom species is the type of water body (Dokulil and Teubner, 2000). In temperate regions, large shallow lakes such as Lake Taihu in China are conducive to *Microcystis* blooms, while deeper, well-mixed lakes in France are conducive to *Cylindrospermopsis* blooms, and deep, alpine lakes are favourable to *Planktothrix* blooms (Dokulil and Teubner, 2000). There were three main types of water bodies in the present metadata, natural lakes, artificial reservoirs, and ponds. There was a significant difference in bloom genera between lakes and reservoirs (Fig. 7, P-value=0.001*<0.05), with *Microcystis* blooms found in more natural lakes than reservoirs and *Cylindrospermopsis* blooms found in more reservoirs than natural lakes, as indicated in Fig. 7 by the clear separation between two ellipses. This could be due to the difference in structure of tropical lakes and reservoirs. Natural lakes usually discharge surface water but reservoirs can have outlets at different depths and thus, this may affect the outflow of the water body (Ji, 2008). Most reservoirs may encounter extreme fluctuations in water level depending on water usage, while natural lakes tend to have less extreme fluctuations in water level and very little control of discharge depth (Ji, 2008). Greater mixing and higher turbidity of the mixed layer in reservoirs and could lead to more *Cylindrospermopsis* blooms, especially in times of drought (Bouvy *et al*., 2000). Stable water conditions and limited changes in discharge depths combined with high nutrients may lead to a higher occurrence of *Microcystis* blooms in natural lakes (Baldia *et al*., 2003). However, it is important to note that the studies used in this meta-analysis may not be representative of all tropical lakes and reservoirs. The effect of ponds could not be discerned in this analysis, as there was only one pond out of the 48 water bodies selected. However, similar genera were present in this pond compared to the other water body types.

Other factors such as light intensity and stratification of the lakes were not taken into account for this meta-analysis due to the lack of detailed information on light and temperature profiles of the water bodies. Flushing of water bodies was not analysed in this meta-analysis due to the lack of detailed information for flushing rates of different water bodies. Poste *et al*. (2013) showed that higher flushing rates of Napolean Gulf in Lake Victoria had led to a lower biomass of *Microcystis* compared to other less flushed sites such as Lake George and Lake Saka in Uganda. However, the rate of flushing and difference in biomass was not quantified and thus, higher flushing in combination with other factors may have caused the lower biomass of *Microcystis*. Jayatissa *et al*. (2006) did note a decrease in cyanobacterial blooms in Sri Lanka due to flushing and dilution of water after heavy rains. However, this study noted that cell density of *Micro-*

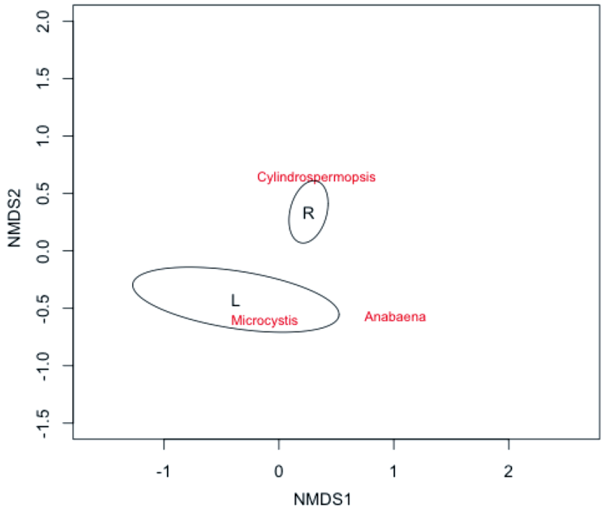

Fig. 7. Non-metric multidimensional scaling of tropical cyanobacterial blooms overlayed with ellipses indicating types of water bodies (L, lakes; R, reservoirs; P-value=0.001;*<0.05).

cystis remained high even without scum formation throughout the wet and dry seasons. Retention time was indicated as an important variable in determining the biomass of cyanobacteria in Funil Reservoir in Brazil (Soares *et al*., 2012). In Barra Bonita reservoir, cyanobacterial biomass was recorded during both short and long retention times and in highly stratified and destratified conditions, indicating that nutrient availability was more important than flushing (Dellamano-Oliveira *et al*., 2008). Overall, flushing and retention time of a tropical reservoir may be important in determining biomass in the surface water, however, nutrients may play a larger role in determining biomass growth in the entire water body throughout the year.

Effects of nutrient levels on microcystin production

Nitrogen concentration was found to be one of the more important factors influencing tropical *Microcystis* bloom formation (Fig. 6). Cyanobacterial blooms in tropical countries occurred over a wide range of N:P ratios. The N:P values found in tropical lakes with the highest microcystin values appear to be similar to those in temperate lakes at approximately 20 (Orihel *et al*., 2012) (Fig. 8). It was found that as N:P (nitrate:phosphate) values increased, the level of microcystins increased significantly (Spearman's rank correlation, ρ=0.746, P-value=0.002 <P_{crit} 0.05) for microcystin levels higher than 1 μg L^{-1} (R Core Team 2012) (Fig. 8). There are distinct geographical patterns present in the level of N:P (nitrate:phosphate) and microcystins encountered in the tropics, with African blooms having lower microcystin values and N:P (nitrate:phosphate) ratios recorded compared to blooms in Asia and Australia (Fig. 8). This could be due to an artefact in the timing of the data collection (snapshot data *vs* long term data) and not purely due to a lower N:P (nitrate:phosphate) ratio present in African water bodies (Chia *et al*., 2009). However, it is important to note that the data analysed were taken from studies that documented microcystin concentration as well as nitrate and phosphate levels. Some studies that documented high microcystin concentrations (>3 μg L^{-1}; Addico *et al*., 2006) did not document nitrate or phosphate levels and thus could not be taken into account for this analysis. Also, studies that documented the presence of microcystins without quantification could not be accounted for (Odokuma and Isirima, 2007; Haande *et al*., 2007).

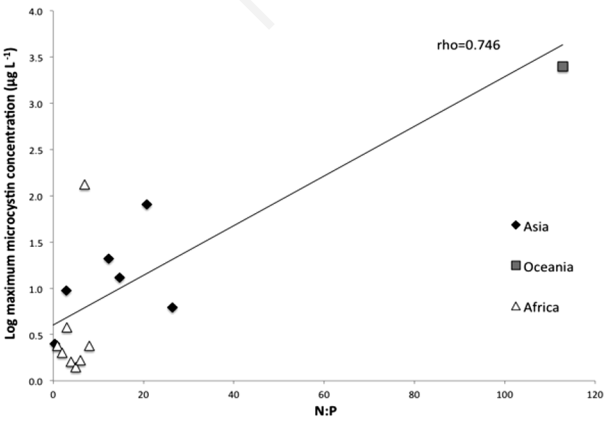

Fig. 8. Log maximum microcystin concentrations (μg L^{-1}) at different N:P values in tropical lakes and reservoirs. Cyanobacterial blooms with less than 1 μg L^{-1} of microcystin recorded were not included in this analysis.

However, it is important to note that the N:P (nitrate:phosphate) ratio alone is not the only factor influencing the level of microcystin production by cyanobacteria. Different strains and species of microcystin-producing cyanobacteria respond differently to individual changes in concentrations of nitrogen and phosphorus (de Figueiredo *et al*., 2004). The data on nutrient levels in tropical lakes and reservoirs are also sparse and thus the relationship between N:P (nitrate:phosphate) ratios and microcystin production in tropical countries cannot be fully explored. Different species and strains of cyanobacteria can also have differing levels of microcystin production based on other factors such as temperature.

Effect of temperature on microcystin concentration

Increased temperatures in temperate countries can lead to more toxic strains developing and outcompeting non-toxic strains of *Microcystis* (Briand *et al*., 2008; Davis *et al*., 2009). The higher gene copy of microcystin synthetase genes (McyD) in *Microcystis* species at elevated temperatures could mean increased toxicity of cyanobacterial blooms under warmer conditions (Davis *et al*., 2009). However, this trend has yet to be found in tropical water bodies and Spearman's correlation analysis on the maximum temperatures of water bodies and total microcystin concentration based on 11 papers and 17 water bodies, did not yield significant results (ρ=0.318, P-value=0.229>P_{crit} 0.05). Studies that did not document the maximum temperatures for individual water bodies were excluded and thus, there is a certain bias in the results that could have led to this insignificant effect of temperature. However, temperature ranges in the tropics are within 1-8°C for each water body (Ahmed *et al*., 2008; Wang *et al*., 2002; White *et al*., 2003; Kotut *et al*., 2010) and this small increase in temperature, which was within the optimum temperature range of *Microcystis* toxin production (25-30°C, Van der Westhuizen and Eloff, 1985; Kim *et al*., 2005), may not significantly affect toxicity.

Effect of microcystis biomass on microcystin concentration

The concentration of cyanobacteria may also influence microcystin levels. Studies in temperate, sub-tropical as

well as tropical countries have found positive correlations between the concentration of microcystin and the concentration of cyanobacteria in blooms (Xu *et al*., 2008; Poste *et al*., 2013). Our analysis across tropical American and Asian regions also showed microcystins to significantly increase (Spearman's rank correlation, ρ=0.94, P-value=0.017*<P_{crit} 0.05) with increasing concentration of *Microcystis* spp. (R Core Team 2012) (Fig. 9). However, this trend was clear only for toxin concentrations higher than 1 µg L^{-1}. Concentrations of blooms from tropical American and Asian countries containing known toxic strains of cyanobacteria can possibly be used to estimate microcystin levels in areas where regular toxin testing is unavailable or unaffordable. This correlation was not significant for tropical African blooms (Spearman's rank correlation, ρ=0.373, P-value=0.153 >P_{crit} 0.05), where tropical African blooms had lower microcystin concentration per cell concentration as compared to tropical Asian and American blooms (Fig. 9). The lower microcystin concentration per cell in African lakes was based on a limited amount of studies and could be a result of the infrequent sampling and short time periods sampled (monthly for 1 year, Okello *et al*., 2010; monthly for 6 months, Poste *et al*., 2013). Data collected bimonthly and over a longer period of time should be more indicative of the trends. Also, Okello *et al*. (2011) found that there was significant within site variation of microcystin production per *Microcystis* cell for lakes in Uganda and that average microcystin per cell was dependent on the proportion of *mcyB* genotype of *Microcystis* more than direct cell counts. However, this trend was not clear in other tropical water bodies. Vasconselos *et al*. (2010) indicated that even though *mcyB* was present in a Mexican lake sample, there was zero microcystins detected and similarly, another lake that had zero *mcyB* detected, had microcystins detected. Thus, there is no clear indicator of microcystin content in water bodies across the tropics but each water body should have its own guideline for either *mcyB* genotypes or *Microcystis* cells, depending on which factor has better predictive power. The variation of microcystin production by *Microcystis* has also been noted in temperate blooms where time and location were important factors in determining microcystin production within a connected freshwater ecosystem (Sabart *et al*., 2010). Another important note about this correlation analysis is that it was based on a limited number of studies and water bodies and in order to improve its applicability and context, more studies with higher frequency of sampling over longer periods of time should be added.

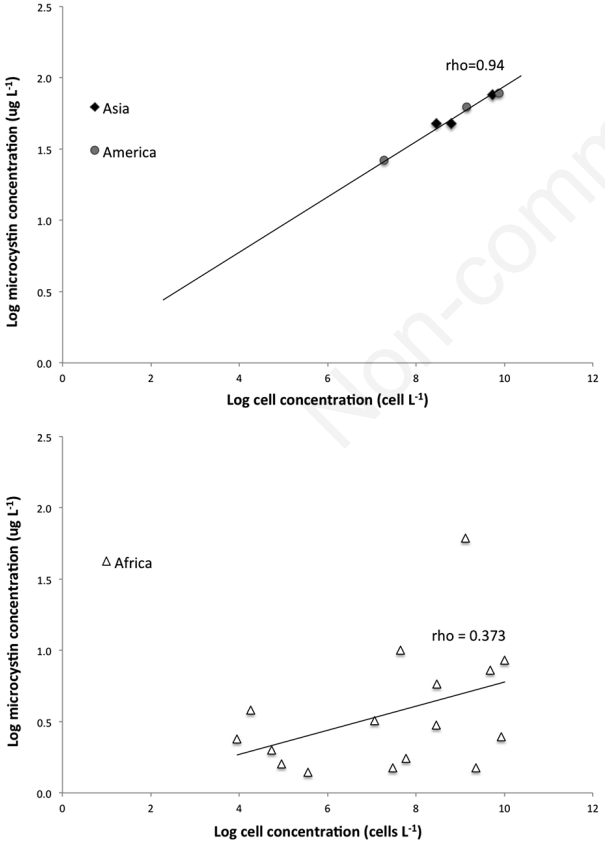

Fig. 9. Log microcystin concentrations (µg L^{-1}) plotted against log cell abundance (cells L^{-1}) for different cyanobacterial blooms in the tropics. Cyanobacterial blooms with less than 1 µg L^{-1} of microcystin recorded were not included in this analysis.

CONCLUSIONS

It is important to understand the prevailing patterns or trends of toxic cyanobacterial blooms in the tropics as these may differ from the more widely studied temperate and subtropical regions. Across the tropics, the genus *Microcystis* was the most prevalent bloom-forming cyanobacteria, followed by *Cylindrospermopsis*, with fewer blooms formed by *Anabaena* and *Planktothrix*. However, different tropical regions were also characterized by different bloom-forming species such as *Cylindrospermopsis* spp. being more prevalent in tropical Australia and Brazil, and *Microcystis* spp. more so in Asia, Africa and Central America. Microcystins were the most frequently encountered toxins, while cylindrospermopsins, anatoxins and saxitoxins were detected in fewer water bodies in tropical areas.

Various studies showed that *Cylindrospermopsis* blooms were more likely to occur in the dry season as compared to the wet season in the tropics while *Microcystis* blooms were found to bloom during the wet season after heavy rain.

Based on our meta-analysis, increasing total nitrogen levels were related to more *Microcystis* blooms and higher maximum temperatures were associated with more *Cylin-*

drospermopsis blooms. Tropical lakes were significantly associated with *Microcystis* blooms while tropical reservoirs were significantly associated with *Cylindrospermopsis* blooms. Microcystin levels from *Microcystis* blooms were found to have a positive relationship with N:P (nitrate:phosphate) ratios across the tropics. Tropical African blooms were found to have no significant correlation between microcystin concentration and cell concentration as compared to Asian and American blooms, which showed significant positive correlation between microcystin concentration and cell concentration. Concentrations of blooms from tropical Asian and American countries containing known toxic strains of cyanobacteria can possibly be used to estimate microcystin levels in areas where regular toxin testing is unavailable or unaffordable. Maximum temperature of tropical water bodies did not have a significant effect on total microcystin concentrations, which may be due to the warmer temperatures experienced being within the optimum temperature range for microcystin production.

Although, the results from our meta-analysis and correlation analysis agree with the general literature on cyanobacterial blooms, it is important to note that all the analyses were based on small subsets of the total literature found on tropical countries, and that there were many water bodies without information that were not included. There could also be possible bias of data due to low frequency of sampling and short sampling duration in several studies. Thus, more information about cyanobacterial blooms in tropical countries is still needed to gain further insights into their patterns of occurrence, toxin production and causes of blooms.

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