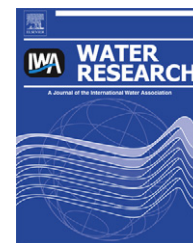


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Review

Effects of rainfall patterns on toxic cyanobacterial blooms in a changing climate: Between simplistic scenarios and complex dynamics

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ABSTRACT

Toxic cyanobacterial blooms represent a serious hazard to environmental and human health, and the management and restoration of affected waterbodies can be challenging. While cyanobacterial blooms are already a frequent occurrence, in the future their incidence and severity are predicted to increase due to climate change. Climate change is predicted to lead to increased temperature and changes in rainfall patterns, which will both have a significant impact on inland water resources. While many studies indicate that a higher temperature will favour cyanobacterial bloom occurrences, **the impact of changed rainfall patterns is widely under-researched and therefore less understood.**

This review synthesizes the predicted changes in rainfall patterns and their potential impact on inland waterbodies, and identifies mechanisms that influence the occurrence and severity of toxic cyanobacterial blooms.

It is predicted that there will be a higher frequency and intensity of rainfall events with longer drought periods in between. Such changes in the rainfall patterns will lead to favourable conditions for cyanobacterial growth due to a greater nutrient input into waterbodies during heavy rainfall events, combined with potentially longer periods of high evaporation and stratification. These conditions are likely to lead to an acceleration of the eutrophication process and prolonged warm periods without mixing of the water column. **However, the frequent occurrence of heavy rain events can also lead to a temporary disruption of cyanobacterial blooms due to flushing and de-stratification, and large storm events have been shown to have a long-term negative effect on cyanobacterial blooms. In contrast, a higher number of small rainfall events or wet days can lead to proliferation of cyanobacteria, as they can rapidly use nutrients that are added during rainfall events, especially if stratification remains unchanged.**

With rainfall patterns changing, cyanobacterial toxin concentration in waterbodies is expected to increase. Firstly, this is due to accelerated eutrophication which supports higher cyanobacterial biomass. Secondly, predicted changes in rainfall patterns produce more favourable growth conditions for cyanobacteria, which is likely to increase the toxin production rate. However, the toxin concentration in inland waterbodies will also depend on the effect of rainfall events on cyanobacterial strain succession, a process that is still

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little understood. Low light conditions after heavy rainfall events might favour non-toxic strains, whilst inorganic nutrient input might promote the dominance of toxic strains in blooms. This review emphasizes that the impact of changes in rainfall patterns is very complex and will strongly depend on the site-specific dynamics, cyanobacterial species composition and cyanobacterial strain succession. More effort is needed to understand the relationship between rainfall patterns and cyanobacterial bloom dynamics, and in particular toxin production, to be able to assess and mediate the significant threat cyanobacterial blooms pose to our water resources.

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Abbreviations – nutrients

C	carbon
CO ₂	carbon dioxide
DIC	dissolved inorganic carbon
DOC	dissolved organic carbon
N	nitrogen
NH ₄	ammonium
NO ₃	nitrate
P	phosphorous
TN	total nitrogen
TP	total phosphorous

Abbreviations – cyanobacterial species

<i>A. flos-aquae</i>	<i>Aphanizomenon flos-aquae</i>
<i>A. planctonica</i>	<i>Anabaena planctonica</i>
<i>A. raciborskii</i>	<i>Anabaenopsis raciborskii</i>
<i>C. raciborskii</i>	<i>Cylindrospermopsis raciborskii</i>
<i>M. aeruginosa</i>	<i>Microcystis aeruginosa</i>
<i>O. agardhii</i>	<i>Oscillatoria agardhii</i>
<i>R. cf. mediterranea</i>	<i>Raphidiopsis cf. mediterranea</i>
<i>W. naegeliana</i>	<i>Woronichinia naegeliana</i>
<i>W. compacta</i>	<i>Woronichinia compacta</i>

1. Introduction

Water as a natural resource provides important ecosystem services such as the delivery of water for drinking and irrigation, and waterbodies for recreational use to the human population (Cosgrove and Rijsberman, 2000; Millennium Ecosystem Assessment, 2005). Therefore, adequate management of water resources is of utmost importance for sustaining the growing world population in the future. In recent decades, the health of freshwater systems has already been compromised due to excessive nutrient input, increased water abstraction, and pollution. Toxic cyanobacterial blooms are one of the most serious symptoms of this and cause severe health issues and

increased financial pressure (Carmichael, 2001; Chorus and Bartram, 1999; Ghadouani and Coggins, 2011; WHO, 2003).

The fourth assessment report of the Intergovernmental Panel on Climate Change (IPCC, 2007a) anticipates that an increase in average temperature is likely to lead to a higher frequency of toxic cyanobacterial blooms in the future. There is some consensus on the fact that “blooms like it hot” (Paerl and Huisman, 2008), and this idea may have led to the generation of a simplistic explanation based solely on an average increase in water temperature. However, the various processes involved in the formation of algal blooms (with or without toxin production) are complex ecosystem processes, and despite many attempts are still barely understood. The difficulties are usually

associated with the fact that the possible causes of algal blooms can be of biotic or abiotic nature, depend on the species community, and are usually site specific (Anderson et al., 2002; Sinang et al., under revision).

In addition to the increase in water temperature, changes in the large-scale hydrological cycle are evident through a greater variability in the spatial and temporal distribution in rainfall (IPCC, 2007b), but very little is known about the effect of changes in rainfall patterns on the occurrence of cyanobacterial blooms. The predicted changes in precipitation patterns can strongly influence water quality (Codd, 2000) by changing the hydrology of inland waters, which leads to different mobilization or dilution rates of nutrients and changes in the physical conditions in waterbodies.

The effects of rainfall intensity, rainfall frequency, and length of dry periods on the occurrence, severity, and toxin production of cyanobacterial blooms are yet to be elucidated. While previous studies have suggested that the changes in rainfall may severely promote the occurrence of cyanobacteria (Shaw et al., 2001), the mechanism behind these impacts is not well understood. Rainfall events represent disturbances to waterbodies by initiating a change in the environmental

factors that influence eutrophication and bloom occurrence. For instance, modelling of the first recorded *Microcystis aeruginosa* bloom in the Swan River (Western Australia), after a heavy summer rainfall event in 2000, indicated that the bloom could have established due to a combination of reduced salinity of this usually brackish to saline river with simultaneous high nutrient input, high water temperature and high insolation (Robson and Hamilton, 2003).

In general, changes in the physicochemical conditions in aquatic systems caused by rainfall events will mainly depend on the characteristics of the respective event, the hydrology of the catchment and waterbody, and the land use in the catchment area. The extent of this disturbance on cyanobacterial blooms in turn is a complex direct function of these physicochemical changes of water parameters (e.g., temperature, nutrients, light, conductivity) on cyanobacteria, a complex indirect function of the physicochemical changes on predators and competitors of cyanobacteria, and might strongly depend on the trophic status of systems (Noges et al., 2011) (Figs. 1 and 2). In principle and in the absence of nutrient limitation, higher nutrient concentrations in eutrophic systems lead to higher carrying capacities and biomass production; this

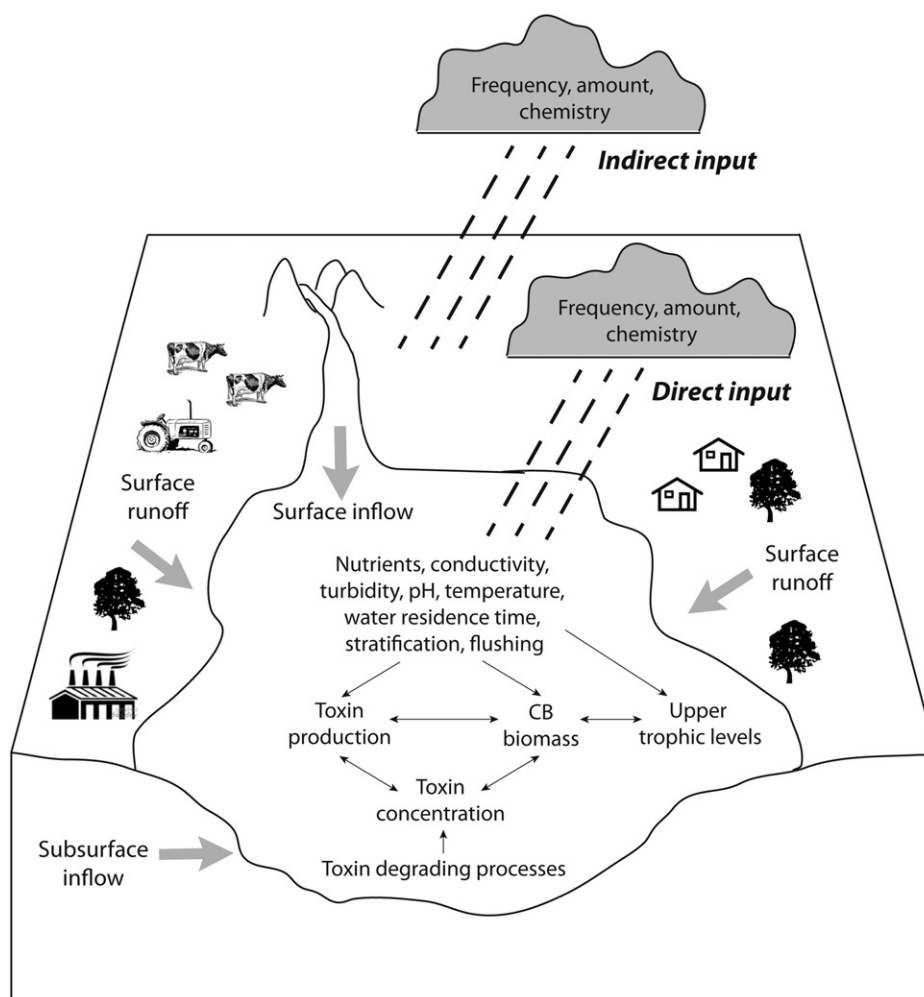


Fig. 1 – Conceptual diagram showing the different pathways of water flowing into inland waterbodies during and after rainfall events, and the physical, chemical and biological parameters that potentially affect cyanobacterial bloom dynamics, toxin production, and total toxin concentration in an inland waterbody. For more details on important food web interactions, see Fig. 2.

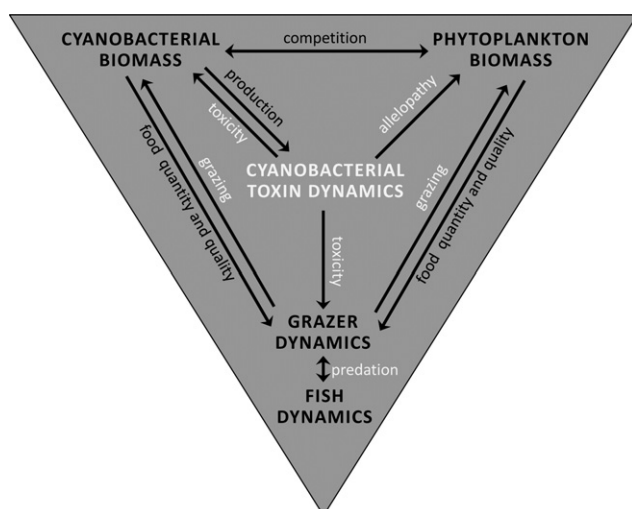


Fig. 2 – Conceptual model showing the complex interactions leading to the cyanobacterial toxin dynamics in waterbodies. The model indicates the connection between the direct (black letters) and indirect (grey letters) effects of physicochemical changes in the waterbody caused by rainfall events on cyanobacterial biomass, cyanobacterial toxin production, phytoplankton, grazer (e.g., zooplankton), and higher trophic level (e.g., fish) dynamics, and on the respective interactions.

eutrophication process generally favours the occurrence of potentially toxic cyanobacterial biomass due to their higher affinity to nutrients compared to other phytoplankton (Chorus and Bartram, 1999), and their ability to adjust their buoyancy and therefore exploit nutrients, light and inorganic carbon resources over a wider range (Paerl et al., 2011; Wagner and Adrian, 2009). Additionally, some cyanobacterial species are equipped with nitrogen fixation ability (Chorus and Mur, 1999).

The effects of predicted changes in rainfall patterns on bloom dynamics are hard to assess with our current knowledge, as direct studies between rainfall and cyanobacterial blooms in freshwater systems are relatively scarce in the literature. Furthermore, there is very limited information about the direct effects of rainfall events on toxin production, and thus toxin concentration in the waterbodies. Many cyanobacterial species can produce toxins that are hazardous to wildlife, livestock and humans (Chorus and Bartram, 1999; Stewart et al., 2007). Although this problem was identified more than 130 years ago (Carmichael, 2008; Francis, 1878), management strategies still fail to reliably predict the toxicity of blooms. Reasons for this are manifold and are related to the complex interaction of physicochemical factors that not only affect toxin production within a cyanobacterial cell, but also the succession of toxic and non-toxic cyanobacterial species and strains. With toxins being a significant threat to ecosystems and humans, this is a serious knowledge gap that needs to be urgently addressed.

The overall aim of this review is to build an understanding of how changes in rainfall patterns will affect the occurrence, severity and toxicity of cyanobacterial blooms in the future. To achieve this, we critically review the existing literature on the effects of rainfall events on cyanobacterial blooms,

summarize how rainfall patterns are predicted to change, and address important information on how the frequency and intensity of rainfall events affect physicochemical conditions in inland waterbodies. We also discuss the role of land use as an important factor influencing the effect of rainfall events on waterbodies. An additional overview of the most important physicochemical factors that affect cyanobacterial growth and toxin production makes this review a holistic synthesis that leads to the suggestion of a conceptual model of the effect of rainfall on cyanobacterial blooms and ecosystems. This model also integrates the toxicity of lakes as one of the most important challenges with regard to cyanobacterial bloom management, and identifies gaps that urgently need to be addressed in future studies.

2. Global and regional predictions of changes in rainfall characteristics

Rainfall events are categorized by their intensity and frequency (Davis and McCuen, 2005). The intensity is expressed as the amount (volume) divided by the duration (i.e., mm hr^{-1}) of an event. The frequency is defined as the frequency of occurrences of events with the same intensity. A comprehensive review of the drivers and the estimation of likely changes in precipitation distribution is given by the fourth assessment report of the Intergovernmental Panel on Climate Change (IPCC, 2007b) (Table 1). Here, we give a general overview of the predicted changes in precipitation patterns that are likely to have an effect on cyanobacterial bloom dynamics.

With global warming, it is expected that the total amount of rainfall will increase; however the observed trend for the global annual land mean precipitation depends on the period it is calculated from, due to a high inter-decadal variability (positive trend for 1901–2005, negative trend for 1951–2005) and on the region from which the data was sourced (Table 1) (IPCC, 2007b). On a global scale, it is predicted that the frequency of extreme rainfall events will change more dramatically than the mean precipitation rate (Allen and Ingram, 2002; IPCC, 2007b); heavy rainfall events are predicted to occur more often in the near future while the amount of total precipitation is predicted to change only slowly. The increase in frequency is even likely for regions where a reduction or no change in the total amount of rainfall is predicted (Alpert et al., 2002; Brunetti et al., 2004; Easterling et al., 2000; Groisman et al., 2005; Yu and Neil, 1993). This will lead to prolonged dry periods in between events (Groisman and Knight, 2008), and the probability for droughts is predicted to increase, especially in mid-continental areas during summer (Meehl et al., 2007). The mean intensity of events has also increased worldwide and this trend is especially pronounced for very heavy and extreme days of rain (Brunetti et al., 2004; De Toffol et al., 2009; Karl and Knight, 1998).

3. The relationship between rainfall events and cyanobacterial dynamics

The development of cyanobacterial blooms is a function of complex interactions between physical, chemical and

Table 1 – Summary of projected regional change in precipitation patterns over the 21st century. The findings take into account the uncertainties in climate sensitivity (i.e. the response of climate to changes in forces) and emission trajectories (e.g., for CO₂, temperature) and are assessed as likely (> 66% probability) or very likely (> 90% probability) (after Christensen et al., 2007).

Country	Amount of annual rainfall
Africa	
Mediterranean Africa, the northern Sahara, southern Africa	likely to decrease
East Africa	likely to increase
Europe	
Northern Europe	very likely to increase ^a
Mediterranean area	very likely to decrease ^b
Central Europe	likely to increase in winter ^c likely to decrease in summer
Asia	
Northern Asia	very likely to increase in winter likely to increase in summer
Tibetan Plateau	very likely to increase in winter
East Asia	likely to increase ^d
Southeast Asia	likely to increase ^d
South Asia	likely to increase
Central Asia	likely to decrease
North America	
Canada	very likely to increase
Northeast USA	very likely to increase
Southwest USA	likely to decrease
Central and South America	
Central America	likely to decrease
Southern Andes	likely to decrease
Tierra del Fuego	likely to increase in winter
South-eastern South America	likely to increase in summer
Australia and New Zealand	
Southern Australia	likely to decrease ^e
South-western Australia	very likely to decrease in winter
West coast of South Island of NZ	likely to increase
Australia except southern Australia	^e
New Zealand	^e
Small Islands	
Greater Antilles	likely to decrease in summer
Seychelles	likely to increase (Dec–Feb)
Maldives	likely to increase (June–Aug)
Mauritius	likely to decrease (June–Aug)
Equatorial Pacific	likely to increase
Additional predictions:	
a Extremes of daily precipitation very likely to increase.	
b Annual number of precipitation days very likely to decrease and risk of summer drought likely to increase.	
c Risk of summer drought likely to increase.	
d Frequency of intense precipitation events very likely to increase.	
e Extremes of daily precipitation very likely to increase.	

biological factors in the waterbody. These factors can be affected by rainfall events; however the ultimate effect on them depends upon the interplay between the quantity and quality of the inflowing water during and after rainfall events, the volume ratios of inflowing to receiving water, the seasonal

timing of the event, and in-lake conditions (Noges et al., 2011) (Fig. 1). All these are again complex functions of the amount of rainfall, the intensity of the event, the length of the preceding dry period, the geology, hydrology and size of the catchment area, the land use in the catchment area, and the chemistry of the rainwater. In order to understand how changes in rainfall patterns will affect cyanobacterial bloom dynamics, it is important to identify how each of these factors changes those conditions in waterbodies that ultimately affect the occurrence of cyanobacteria.

During rainfall events, water enters the waterbody directly by wet deposition and indirectly by runoff, surface and subsurface flows (Fig. 1), changing the conditions within the waterbody. While the effect of wet deposition is immediate as rainwater mixes with lake water during the rainfall, the impact of water entering the waterbody indirectly via groundwater or surface water might take hours to years (Alvarez-Cobelas et al., 2006), depending on the size of the catchment area and the geology (Winter, 1999). Additionally, while wet deposition will enter the waterbody chemically and physically unchanged, the rainwater that enters the waterbody indirectly will be modified by physical and biological processes (Heathwaite and Johnes, 1996), and will usually transport large amounts of nutrients to the waterbodies.

Information about the effect of changes in the physico-chemical condition of the waterbody on cyanobacteria is plentiful, both from field and laboratory experiments. The effect was shown to be highly species and strain specific and has been discussed and reviewed extensively elsewhere (Camargo and Alonso, 2006; Chorus and Bartram, 1999; Reynolds and Walsby, 1975). In general, cyanobacterial growth is enhanced and cyanobacteria are superior competitors against other phytoplankton at high temperature and conductivity, and under nutrient-rich and stratified conditions. Buoyant cyanobacteria are highly favoured during periods of high turbidity and high pH due to their ability to stay close to the surface where they are able to harvest light and CO₂ (which is usually low in water with high photosynthesis rates and thus pH > 9) from the atmosphere (c.f. Paerl et al., 2011; Reynolds and Walsby, 1975). However, the effect of nutrients on cyanobacterial growth is partially contradictory, emphasizing that the response will strongly depend on the interaction of different nutrients, and that the competitive advantage of cyanobacteria over other phytoplankton will be highly system-specific (c.f. Davies et al., 2010; Shaw et al., 2001). For instance, many studies emphasize the importance of low N:P or NO₃–N:TP ratios for the occurrence of cyanobacterial blooms (Chorus and Mur, 1999; Guildford and Hecky, 2000; McQueen and Lean, 1987; Smith, 1983), however this might be a prerequisite rather than a cause for cyanobacterial blooms as many waterbodies with low ratios do not exhibit blooms (An and Jones, 2000a; Bouvy et al., 1999; Smith, 1983).

4. Effects of rainfall patterns on cyanobacterial dynamics

To date, there are few studies that have directly measured the effect of rainfall events on cyanobacteria in freshwater systems (Table 2). Most of these studies were conducted in

Table 2 – Summary of studies that investigated the response of cyanobacteria, phytoplankton and ecosystems to rainfall events in lakes and reservoirs.

Indicator	Effect	Potential driver(s)	System type	Reference
• <i>Microcystis</i>	• High biomass	• Rainfall caused mixing and re-suspension of <i>Microcystis</i> cells from the sediment	Lake	(Kebede and Belay, 1994)
• <i>A. raciborskii</i>	• Bloom	• Nutrient inflow by rainfall and subsequent windless warm days	Shallow lake	(Toth and Padisak, 1986)
• <i>Arthrospira</i> , <i>Oscillatoria</i> , <i>Spirulina</i>	• Mixed bloom	• Rainfall caused reduced salinity and increased nutrient concentrations	Saline lake	(Badve et al., 1993)
• <i>A. flos-aquae</i>	• Bloom	• Drought caused a decreased depth of mixed layer with sufficient nutrient concentration	Reservoir	(Vasconcelos, 1991)
• <i>Cylindrospermopsis</i>	• Bloom	• Drought caused long water residence time, eutrophic conditions, reduced light transparency	Reservoir	(Bouvy et al., 1999)
• <i>C. raciborskii</i> , <i>R. cf. mediterranea</i>	• Mixed bloom	• Drought caused stable water column, high conductivity, low light availability; an efficient alkalinity system allowed cyanobacteria the use inorganic carbon	Reservoir	(Bouvy et al., 2003)
• <i>A. flos-aquae</i> , <i>M. aeruginosa</i> , <i>O. agardhii</i>	• Mixed surface scum	• Periods without rainfall and low wind velocity	Lake	(Soranno, 1997)
• <i>Microcystis</i> , <i>Anabaena</i>	• Increase in biomass	• Drought caused prolonged periods of high surface water temperature, stable stratification and nutrient release from sediment in anoxic hypolimnion	Reservoir	(Jones and Poplawski, 1998)
• <i>Microcystis</i> , <i>Anabaena</i>	• Mixed bloom	• Drought caused strong thermal stratification and long water residence time	Reservoir	(An and Jones, 2000a, b)
• <i>A. circinalis</i> , <i>A. flos-aquae</i> , <i>Microcystis</i>	• Decrease in biomass	• Rainfall caused increased turbidity and high turbulence	Shallow lake	(James et al., 2008)
• <i>Lyngba</i> , <i>Planktolyngba</i>	• Increase in biomass	• Rainfall caused increased turbidity and high turbulence	Shallow lake	(James et al., 2008)
• <i>A. flos-aquae</i>	• Collapse of bloom	• Rainfall caused flushing and de-stratification	Shallow lake	(Jacobsen and Simonsen, 1993)
• <i>Microcystis</i> , <i>Anabaena</i>	• Decrease in biomass	• Mixing or increased turbidity or changes in other physicochemical factors caused by rainfall	Reservoir	(Jones and Poplawski, 1998)
• <i>Microcystis</i> , <i>Anabaena</i>	• Decrease in biomass	• Rainfall caused lower irradiance	Reservoir	(Ahn et al., 2002)
• <i>Microcystis</i> , <i>Anabaena</i>	• Lower frequency and magnitude of blooms	• Extreme rainfall caused flushing during intense monsoon years	Reservoir	(An and Jones, 2000a, b)
• Filamentous cyanobacteria	• Decrease in biomass	• Rainfall caused mixing and increase in total inorganic N (especially NO ₃ -N)	Lake	(Tryfon et al., 1994)
• <i>Anabaena</i> , <i>A. planctonica</i> , <i>Radiocystis</i> , <i>W. naegeliana</i> , <i>W. compacta</i> , <i>Aphanothece</i>	• Interruption of bloom occurrences	• Appearance of a dinoflagellate bloom due to wet winter	Eutrophic lake	(Noges et al., 2011)
• <i>C. raciborskii</i>	• No change in dominance	• Intrinsic factors more important than environmental factors	Reservoir	(Figueredo and Giani, 2009)
• Total algal biomass	• Increase directly after rainfall periods	• Mixing and higher nutrient concentrations	Lake	(Kebede and Belay, 1994)
• Total algal biomass	• Increase	• Increased nutrient concentrations due to wet winter	Oligotrophic lake	(Noges et al., 2011)
• Algal blooms	• Reduced occurrence	• Rainfall caused increased turbidity and high turbulence	Shallow lake	(James et al., 2008)
• Total algal biomass	• Decrease	• no explanation given	Pond	(Khondker and Kabir, 1995)

(continued on next page)

Table 2 – (continued)

Indicator	Effect	Potential driver(s)	System type	Reference
• Total algal biomass	• Decrease	• Rainfall caused dilution	Reservoir	(Figueredo and Giani, 2001)
• Total algal biomass	• Decrease	• Rainfall caused flushing	Reservoir	(Bouvy et al., 2003)
• Total algal biomass	• Decrease	• Rainfall caused mixing and flushing	Reservoir	(Harris and Baxter, 1996)
• Algal community	• Higher diversity	• Rainfall caused de-stratification	Shallow lake	(Jacobsen and Simonsen, 1993)
• Algal community	• Higher diversity	• Rainfall caused instability of system, disturbance	Reservoir	(Figueredo and Giani, 2001)
• Algal community	• Higher diversity at low chlorophyll levels	• Rainfall caused disturbed conditions and collapse of bloom	Reservoir	(Bouvy et al., 1999)
• Algal community	• Switch between diatom and cyanobacteria dominance	• Weak monsoon caused SiO ₂ depletion and less mixing	Reservoir	(An and Jones, 2000a, b)
• Rotifers, cyclopoid copepoda	• Dominance during <i>Cylindropermopsis</i> bloom	• These zooplankton can benefit from drought-induced cyanobacterial bloom	Reservoir	(Bouvy et al., 2001)
• Zooplankton biomass	• Increase	• Rainfall caused collapse of <i>Aphanizomenon</i> bloom	Shallow lake	(Jacobsen and Simonsen, 1993)
• Ecosystem	• Weaker trophic interactions	• Flooding destabilizes food webs	Wetland	(Angeler et al., 2000)

reservoirs, probably because of their importance as a drinking water source for humans and the related need to control water quality. In general, these studies indicate that rainfall events might lead to large changes in the physicochemical structure of waterbodies (Bouvy et al., 2003) that translate into changes in phytoplankton communities. In these studies, the most significant effects of rainfall events that influenced cyanobacterial and/or phytoplankton communities were flushing, nutrient input, reduction of conductivity (especially after long dry periods), and mixing of the water column due to water inflow and associated strong winds. In the following, we will summarize these studies in relation to the characteristics of rainfall patterns. Additionally, we will discuss the role of land use on these dynamics, as it is a very important factor influencing the nutrient input to waterbodies during rainfall events.

4.1. How does rainfall intensity affect cyanobacterial biomass dynamics?

The inflow of high volumes of water during rain events can lead to a reduction of algal biomass due to high flushing rates (Bouvy et al., 2003; Figueredo and Giani, 2001, 2009; Jacobsen and Simonsen, 1993; Jones and Poplawski, 1998) and it may take a few days for a bloom to reappear after it has been flushed out by heavy rainfall (Ahn et al., 2002). This is especially relevant after heavy rainfall events. In general, rainfall volume and inflow volume are correlated, however this correlation might only be visible if enough rain falls to saturate the catchment (Harris and Baxter, 1996). Rainfall events can also lead to increased turbidity in waterbodies (Ahn et al., 2002; Figueredo and Giani, 2001; Hart, 2004; Jones and Poplawski, 1998) through sediment input, DOC input (Schindler, 2009), and re-suspension of sediment through storm events (James et al., 2008); this effect can be increased in areas with poor land-management (Hendry et al., 2006). Although suspended solid loadings to waterbodies generally increase with rainfall intensity, they can decrease over time during storm events with a long duration (Deletic and Maksimovic, 1998). While turbidity in general favours cyanobacteria (Paerl et al., 2011), sudden low light availability in combination with turbulence can also lead to a decrease of large-celled cyanobacterial species (James et al., 2008). Especially heavy rainfall events can lead to high turbulence and mixing of the water column (Bouvy et al., 2003; Jones and Poplawski, 1998; Tryfon et al., 1994) by large volume inflow and associated strong wind events, and this was shown to favour non-cyanobacterial species (Bouvy et al., 2003). Thus, in the short term, intense rainfall can lead to a lower total chlorophyll biomass with a higher diversity due to the absence of cyanobacterial dominance (Bouvy et al., 1999). However, in the long term, the increasing nutrient concentrations (e.g., P, N, Fe) in waterbodies during and after rainy periods (James et al., 2008; Kebede and Belay, 1994; Zaw and Chiswell, 1999) will lead to a nutrient enrichment, which not only increases the carrying capacity of biomass of the systems, but also favours cyanobacteria. The quantity of nutrients added to waterbodies during rainfall events strongly depends on the rainfall intensity; compared to low intensity rainfall events, high intensity rainfall events are able to

mobilize and dislodge larger particles and less water infiltrates into the soil leading to runoff being a higher fraction of the rainwater input (Trenberth et al., 2003). Heavy rainfall events, in particular, can lead to massive erosion resulting in very high nutrient input, especially into artificial waterbodies such as reservoirs (Chorus and Mur, 1999), and can input as much as 80% and 400% of the average annual in-lake pools of N and P, respectively (Jones and Poplawski, 1998). While a storm with a higher intensity adds more nutrients to a waterbody than a less intense storm (Budai and Clement, 2007; Davis and McCuen, 2005; Kleinman et al., 2006), the nutrient composition added during high intensity events will be biased towards particulate rather than soluble nutrient forms (Budai and Clement, 2007), as runoff mobilizes mainly particulate nutrients (Gentry et al., 2007). Compared to soluble nutrient forms, particulate nutrients cannot be used directly by primary producers. Therefore, the response of cyanobacterial blooms to nutrient addition will strongly depend on the quality of the nutrients added, which depends not only on the intensity of rainfall events as previously described, but also on the land use, the nutrient concentration in the soil, the soil type, and the watershed transport capacity (D'Arcy and Carignan, 1997; Fraterrigo and Downing, 2008; Kleinman et al., 2006; Lewis and Grimm, 2007). In general, there is a significant positive correlation between human land use and nutrient export from these areas (Bowen and Valiela, 2001a; Bowes et al., 2005; Dillon and Kirchner, 1975; Ham and DeSutter, 1999; Heathwaite and Johnes, 1996; Howarth, 1998; Kato et al., 2009; Le et al., 2010; Soranno et al., 1996; Stow et al., 2001), and between human land use and the ratio of surface to subsurface runoff volume (Bhaduri et al., 2000), with the former being linked to the use of fertilizer, sewage runoff from livestock production areas, urban sewage treatment facilities, and deforestation (Dillon and Kirchner, 1975; Hall et al., 1999; Heathwaite and Johnes, 1996; Jeppesen et al., 2011; Likens et al., 1970). A combination of changes in annual precipitation and forest harvesting can result in enhanced P export into lakes leading to an increased phytoplankton and cyanobacterial biomass (Prepas et al., 2001). The type of land use also influences the nutrient species composition transported to waterbodies. For instance, rainfall events in catchments with livestock export more NH_4 than NO_3 into waterbodies compared to agriculturally affected catchments (Shaw et al., 2001), making blooms more likely in the first as some cyanobacteria seem to be able to take up NH_4 more efficiently (Presing et al., 1996).

A movement of the thermocline by water inflow or winds associated with storms can allow nutrients that are released from sediments to enter the photic zone (Fabbro and Duivenvoorden, 1996), leading to an additional nutrient enrichment. It can also lead to a re-suspension of cells (e.g., *Microcystis* spp.) or dormant forms of cyanobacteria (e.g., akinetes from *Cylindrospermopsis* spp.) into the water column, and previous studies indicated that this encourages bloom development (Fabbro and Duivenvoorden, 1996; Kebede and Belay, 1994).

Conversely, less intense rainfall events can immediately increase cyanobacterial biomass through nutrient enrichment if the event does not lead to de-stratification, as is often the case for isolated rainfall events or in shallow, non-stratified

lakes (Shaw et al., 2001; Toth and Padisak, 1986). Another possible configuration could be that, once a rainfall event ends a dry period, the water becomes enriched with nutrients, while the conductivity decreases (Badve et al., 1993). Especially heavy rainfall events or wet conditions can lead to a significant reduction of the conductivity of waterbodies (Badve et al., 1993; Legesse et al., 2004), as the conductivity of groundwater and rainwater is usually lower than that of most lakes (Gibson et al., 1995). In general, this could lead to a loss of the competitive advantage that cyanobacteria have during long dry periods with higher conductivity (Orr et al., 2004; Tonk et al., 2007). However, the first period after a rainfall event might represent an important time frame that still increases the competitive advantage for cyanobacteria; during this period, the conductivity only decreases slightly, and is therefore still too high for many other phytoplankton species, while there is already a significant first nutrient pulse that can rapidly be used by the cyanobacteria.

The importance of the intensity and amount of rainfall on cyanobacterial blooms was also emphasized by a comparative study in Korea between two years with monsoons of different strength. This study showed that while there was no difference in total chlorophyll between the two years, the taxonomic composition differed with cyanobacteria dominating in the year with the weak monsoon (An and Jones, 2000a).

4.2. How does the length of the preceding dry period affect cyanobacterial biomass dynamics?

In general, rainfall events that terminate long dry spells will lead to a comparably higher pulse of nutrients into waterbodies than rainfall events that occur on a regular basis, as nutrients build up during the no-rain period (Davis and McCuen, 2005; Kleinman et al., 2006), and, during heavy rainfall, rainfall volume is amplified more in runoff from dry than from wet catchments (Chiew et al., 1995). The discharge of nutrients from soils also depends on soil moisture and is again nutrient species dependent (Kato et al., 2009). For instance, water soluble organic forms of P, that can quickly be taken up by algae, are mobilized more easily after longer preceding dry periods, or after drying and rewetting, due to microbial or biochemical processes that facilitate their release (Stutter et al., 2008; Turner and Haygarth, 2001). Therefore, in general, rainfall events that occur after longer dry periods promote conditions in the waterbody that are favourable for cyanobacterial growth.

Additionally, and perhaps more importantly, is the fact that conditions that prevail during prolonged dry periods are themselves very favourable for cyanobacteria. In general, a lower frequency of rainfall events, and therefore prolonged dry periods, leads to increased conductivity due to high evaporation rates (Bonte and Zwolsman, 2010; Bouvy et al., 1999; Bouvy et al., 2003), decreased water levels (Bouvy et al., 1999, 2003; Kebede and Belay, 1994; Kuhn et al., 2011), longer water residence time, non-turbulent and stratified conditions which might increase surface water temperature, and increased release of nutrients (e.g., soluble P, NH_4 , Fe) from the sediment if anoxic hypolimnia develop (Chorus and Mur, 1999). The nutrients released from the sediment can be utilized by buoyant cyanobacteria that are able to control their

vertical movement in the water column (Wagner and Adrian, 2009), and additionally contribute to the eutrophication process during mixing events (Chorus and Bartram, 1999). All these conditions will strongly favour freshwater cyanobacteria (Bouvy et al., 2003; Jones and Poplawski, 1998; Paerl, 1988) with cyanobacterial blooms often dominating during drought and falling water level (Harris and Baxter, 1996), and surface scum often occurring during dry periods with low wind velocities (Soranno, 1997).

An increased conductivity due to evaporation during the dry periods may selectively favour cyanobacteria as many species are more salt tolerant than other phytoplankton species; for example, *M. aeruginosa* long-term growth was not affected by salinity up to 9.8 g L⁻¹ (Orr et al., 2004), with short term tolerance to salinities as high as 17.5 g L⁻¹ (Tonk et al., 2007).

Although the more stable water column during periods of no-rain generally favours filamentous and colonial cyanobacterial species such as *Anabaena*, *Aphanizomenon* and *Microcystis*, as they are promoted during non-mixing phases (c.f. Havens, 2007, c.f. Huisman et al., 2004), *Oscillatoria* growth was shown to be stimulated by mixing events (Reynolds et al., 1984). In regions with distinct dry seasons, blooms prevail longer if the start of the rain is delayed or the rainfall events are too weak to break up the stratification (Shaw et al., 2001).

Prolonged no-rain periods can also lead to lower turbidity in the water and thus higher irradiance penetration. As cyanobacteria are highly adaptive to different light levels this could favour cyanobacterial growth (Shaw et al., 2001). Alternatively, prolonged dry periods can also gradually increase turbidity due to high biomass accumulation, and higher pH due to increased photosynthesis, which would in turn limit DIC in the water column. Both conditions would favour buoyant cyanobacterial species (e.g., *Microcystis*, *Anabaena*, *Planktothrix*) over other phytoplankton as their ability to dwell directly on the surface enables them to avoid DIC limitation (Paerl et al., 2011). High temperatures during prolonged-dry periods also promote high cyanobacterial growth (Chorus and Bartram, 1999). Therefore, many conditions during prolonged dry periods favour cyanobacteria and can lead to lower algal diversity due to cyanobacterial dominance (Bouvy et al., 1999).

The discussion about the effect of the frequency of rainfall events, and as such the length of the preceding dry periods and the intensity of rainfall events, indicates that these two rainfall characteristics have partly contrasting effects on in-lake conditions and mechanisms that directly impact nutrient enrichment of systems ('eutrophication'), and therefore indirectly cyanobacterial bloom dynamics (Table 3). In general, longer dry periods support most conditions that favour nutrient enrichment, while the intensity of rainfall events has an ambiguous impact. This emphasizes that the ultimate effect of changes in rainfall patterns will strongly depend on a combination of intensity and frequency.

4.3. How do changes in the total amount of rainfall affect cyanobacterial biomass dynamics?

Predictions of the changes in the total amount of rainfall vary between regions (Table 1). In general, it can be predicted that a decrease in total rainfall will increase the frequency and intensity of cyanobacterial blooms due to calmer, warmer, more eutrophic conditions, and longer stratification periods. In contrast, an increase in the total amount of rainfall, which is a function of the intensity and frequency of rainfall events, might on average lead to less favourable conditions for cyanobacterial blooms due to shorter water residence times (An and Jones, 2000b; Bouvy et al., 1999). However, the ultimate impact of changes in the total amount of rainfall will depend on the temporal distribution of the rainfall. For example, assuming that the increased amount of rainfall falls evenly over the whole period, this might strengthen the dominance of cyanobacteria, but only if rainfall events are too weak to afflict de-stratification and at the same time add nutrients to the systems. However, if the predicted increase in total rainfall is due to more intense rainfalls, this might interrupt bloom development regularly enough to prevent long-term blooms by flushing and mixing (Noges et al., 2011). Still, in this case, the higher intensity rainfalls will over time lead to a proportionally higher input of nutrients into the system and thus an increased rate of eutrophication, which generally favours cyanobacteria. The ultimate impact of rainfall events on

Table 3 – Correlation between the intensity of rainfall events or the length of dry periods on waterbody conditions or mechanisms that affect these conditions and the direct relationships between these conditions/mechanisms and nutrient enrichment of waterbodies, which will then indirectly affect the occurrence of cyanobacterial blooms. The table should be read as follows: Water residence time is negatively correlated to rainfall intensity and positively to the length of the dry period; water residence time in turn is positively correlated with nutrient enrichment.

Rainfall intensity	Length of dry period	Condition/mechanism	Nutrient enrichment
–	+	Water residence time	+
–	+	Anoxic conditions	+
0 / –	+	Water temperature	0
+ ^a / –	+	Conductivity	0
+	–	Flushing	–
–	+	Water column stability	+ / –
+	+	Nutrient concentrations in the inflow after rainfall	+
+	–	Turbidity through re-suspension of sediment	0
–	+	Turbidity through concentration of biomass	0

a in areas with highly saline groundwater (e.g., South Australia) (Tweed et al., 2009).

blooms through nutrient addition also strongly depends on the trophic status of waterbodies; although nutrient concentration increased significantly after the wet winter in two adjacent temperate lakes with different trophic status, this only led to an increase in phytoplankton biomass in the oligotrophic lake; in the eutrophic lake, biomass decreased and the regularly occurring cyanobacterial blooms were interrupted (Noges et al., 2011).

4.4. Predicted effects of changed rainfall patterns on toxin concentration in the water

Currently, there has been no field study that has directly analysed changes in toxin concentration in the water following rainfall events. However, with toxins being a significant threat to ecosystems and humans, there is an urgent need to advance our understanding. Here, we discuss possible scenarios for changes in the toxin concentration in the water, which are inferred from field and laboratory studies.

Toxin concentration in the water depends on the biomass of toxic cyanobacteria (not necessarily total cyanobacteria), the toxin quota (which relates to toxin production), and toxin degrading processes (Fig. 1). Therefore, it is critical to understand the possible effects that changes in rainfall patterns would have on these processes. It might be easiest to predict the possible effects on toxin production per cell as this is a function of the environmentally influenced gene expression (Chorus and Bartram, 1999). Laboratory experiments with single toxic strains indicate that toxin production within a cell can vary up to 50 fold due to changes in temperature, light, P, N, pH, salinity, and micronutrients, such as iron (reviews: Chorus and Bartram, 1999; Zurawell et al., 2005). The majority of studies indicate that toxin production is positively related to cell growth rate (Briand et al., 2005; Rivasseau et al., 1998; Zurawell et al., 2005). Therefore, if growth conditions are improved by rainfall patterns (e.g., calm, warm and nutrient-rich conditions during prolonged dry periods) this will lead to a higher toxin production rate per cell. However, for iron, it has also been shown that toxin production is enhanced under growth limiting iron conditions (Sevilla et al., 2008). To make this even more complex, each cell can produce more than one toxin variant and changes in environmental factors can lead to production of microcystin variants with differing toxicity. Light limitation (e.g., due to high turbidity after heavy rainfall events) together with excess N and C supply have been shown to enhance the production of the less toxic MC-RR variant (Van de Waal et al., 2009). Therefore, even when an increased production of toxin leads to a higher toxin concentration in the water, it might not necessarily lead to a bloom with higher toxicity.

The second important factor affecting the toxin concentration in the water is the biomass of toxic cyanobacteria (Briand et al., 2008a). In general, if rainfall patterns produce conditions that promote cyanobacterial growth it will lead to higher biomass and consequently higher toxin concentrations in the water; however, this is only true if a bloom consists of a single toxic species, while in reality cyanobacterial blooms often contain a mix of toxic and non-toxic species. Even then, those species that are potentially toxic are comprised of toxic

and non-toxic strains (genetic subgroups of species) (Chorus and Bartram, 1999; Neilan et al., 2008), which might have different optimum growth conditions. For example, non-toxic strains of *M. aeruginosa* were shown to be better competitors for light than toxic strains (Kardinaal et al., 2007), while higher concentrations of inorganic N and P are likely to promote toxic *Microcystis* strains (Davis et al., 2010). It has also been demonstrated that the succession of different strains was responsible for high variations in toxin concentration in the water over the lifetime of a bloom (Blackburn et al., 1997). Therefore, our predictions of the effects of rainfall events on the biomass dynamics of toxic cyanobacteria have to be based on our understanding of toxic and non-toxic species and strain succession. However, in this respect, little is known and results are highly ambiguous, indicating that favourable growth conditions for cyanobacteria can lead to the dominance of non-toxic or toxic strains (Briand et al., 2008a, 2008b, 2005; Davis et al., 2009). Our limited knowledge about the effects of the complex interplay of environmental factors on strain succession makes any prediction of changes in rainfall patterns on the competition between toxic and non-toxic strains very vague.

The third mechanism that influences the total toxin concentration in the water includes processes by which the concentrations of dissolved toxins are decreased. These processes include dilution, biodegradation by bacteria (Chen et al., 2008; Cousins et al., 1996), adsorption onto particulate organic matter and sediments (Rapala et al., 1994), thermal decomposition, and photolysis (Harada and Tsuji, 1998). No direct study of the effects of rainfall events on these processes has been performed, but it can be inferred from the literature that changes in rainfall patterns can have a significant impact on these degrading processes: 1) longer dry periods with high evaporation can lead to increased water temperature that enhances thermal biodegradation and increases bacterial biodegradation (Park et al., 2001); 2) heavy rainfall events that stir up sediment and/or input large amounts of sediment and particulate organic matter could increase the adsorption of toxins to sediment; 3) the input of large water volumes could dilute the dissolved toxin fraction; and 4) changes in pH can lead to changes in the adsorption of toxins onto sediments, with a decreased sorption at higher pH (Wu et al., 2011). Most of these processes would decrease the concentration of dissolved toxins in the water column.

In summary, cyanobacterial toxin concentration in the water is a function of the cyanobacterial biomass, the succession of species and strains, changes in physicochemical conditions, and biodegradation processes. Conditions leading to species-specific proliferation of cyanobacterial cells are fairly well understood, for instance *Oscillatoria* can outcompete other phytoplankton and cyanobacteria under mixed, low light conditions, while *Anabaena*, *Aphanizomenon* and *Microcystis* will dominate under stable conditions with higher underwater irradiance (Havens, 2007). Conversely, the factors that lead to the dominance of toxic or non-toxic strains are still relatively unknown (WHO, 2003). It can be hypothesised that toxin concentration in the water will be higher under future rainfall scenarios due to an increase in cyanobacterial biomass alone (Graham and Jones, 2009). However, higher

biomass does not necessarily mean that growth conditions are optimal for cyanobacteria. It could simply be a result of a higher carrying capacity of a system that was enriched with nutrients by rainfall events. Therefore, whether the average toxin concentration in a waterbody that contains a bloom with a stable ratio of toxic to non-toxic species/strains is increased or decreased by changes in rainfall patterns, even under increased cyanobacterial biomass, will ultimately depend on the effect of rainfall patterns on (variant-) specific toxin production rates (Fig. 3).

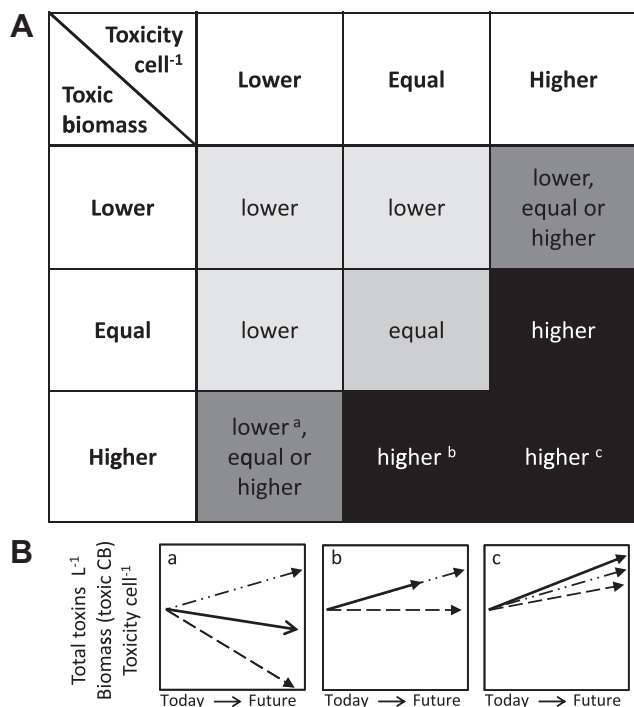


Fig. 3 – (A) Future trends in the total toxin concentration (L⁻¹) in inland waterbodies assessed by using combinations of different levels of toxic cyanobacterial (CB) biomass and toxicity cell⁻¹. For some scenarios (e.g., lower toxicity cell⁻¹ and higher toxin biomass) the outcome will depend on the rates of the respective increase/decrease. (B) The three figure panels relate to the superscripts in (A) and indicate three possible scenarios of the changes in total toxin concentration (solid line) in the waterbodies. A future increase of cyanobacterial biomass (broken lines with dots) due to nutrient enrichment of systems is relatively undisputed in the literature and therefore set equal in all scenarios. The ratio of toxic to non-toxic species/strains within the cyanobacterial biomass is set as fixed. Toxicity of a cell (broken line) will (a) decrease or (c) increase, if less or more toxin is produced (e.g., changes in rainfall patterns that affect growth conditions for cyanobacteria) and/or variants with a lower or higher toxicity are produced respectively. The toxicity of cell will (b) remain stable, if toxin production remains unchanged, if more of less toxic variants are produced (e.g., low light and excess C and N) or if less of more toxic variants are produced. As the total toxin concentration in a lake is a result of the biomass and the toxicity of the cells, it will increase most in (c) and least in (a).

5. Direct effects of wet deposition on cyanobacterial blooms

Nutrient addition to inland waterbodies by direct wet deposition can be significant (Luo et al., 2007a, 2007b; Rogora et al., 2006) and may directly affect primary production and thus also cyanobacterial bloom development (Buijsman and Erisman, 1988; Luo et al., 2007a). Direct deposition of N and P to Lake Taihu (China) by wet deposition alone was calculated as >4700 and 75 t year⁻¹, respectively accounting for 16.5 and 7.3% of the annual N and P input (Luo et al., 2007a, 2007b). The effect of wet deposition becomes more important the lower the input through groundwater or surface water flow (i.e., small catchment area or distant coastal areas) (Jassby et al., 1994; Zhang and Liu, 1994). Especially in closed lakes, nutrient addition through precipitation is the main nutrient source for phytoplankton (Magnuson et al., 1997). However, the chemistry of rainwater is highly variable on a regional and seasonal scale (Kopacek et al., 1997; Luo et al., 2007a; Rogora et al., 2006), with the regional chemical rainfall composition usually reflecting local anthropogenic emissions (e.g., agriculture, industry) (Lara et al., 2010; Luo et al., 2007a; Raper and Lee, 1996; Rogora et al., 2006; Russell et al., 1998; Zhang and Liu, 1994).

The links between wet deposition during rainfall events and primary production have mostly been made for coastal areas (Paerl, 1997; Paerl and Whitall, 1999) and some general understanding can be derived from these. In contrast to freshwater systems, coastal areas are historically believed to be N limited, therefore rainfall, which usually contains more N than P (Paerl et al., 1990), often instantly increases primary production in coastal areas. However, even in freshwater systems, a clear connection between the addition of N and the occurrence of *Microcystis* blooms has been shown (Moisander et al., 2009). In addition, evidence has accumulated that a combination of P and N is important for explaining phytoplankton and cyanobacterial growth (Rabalais, 2002; Smith et al., 1999), and the TN:TP ratio of wet and dry deposition has been identified as an important factor affecting the TN:TP ratio and phytoplankton biomass in alpine lakes (Morales-Baquero et al., 2006). Furthermore, dominance of non-nitrogen fixing cyanobacterial species (e.g., *M. aeruginosa*) depend more on the N:P ratio than on TN (Chorus and Bartram, 1999; Lehman et al., 2009). Therefore, an addition of N through precipitation will also affect systems that are not N-limited by definition, and it has been emphasized that N can play a major role in eutrophic (Davis et al., 2010; Elser et al., 1990; Zhang et al., 2008) and tropical freshwater systems (Downing et al., 1999). This is supported by a recent study which suggested that, while the conditions were already optimal for growth, atmospheric deposition of N and P might have further promoted cyanobacterial blooms (Zhai et al., 2009).

Worldwide, N wet deposition is estimated to have increased by 25–300% between 1910 and 1980, probably due to higher N emissions, but has remained unchanged or decreased since then (Bowen and Valiela, 2001b; Buijsman and Erisman, 1988; Kopacek et al., 1997). These significant changes in rainfall chemistry will without doubt impact bloom

occurrences and intensities, but without further research, little is known about the extent of this effect on inland waterbodies.

6. Longevity of effects of rainfall events on waterbodies

Few studies have investigated the longevity, here defined as how long the effects persist, of rainfall events on phytoplankton community composition and cyanobacterial blooms. Existing studies emphasize a possible long-term effect, especially for large storm events (Harris and Baxter, 1996; James et al., 2008). In one study, flushing of a reservoir by rainfall events decreased phytoplankton biomass significantly for up to three months (Harris and Baxter, 1996) and significantly changed the community composition. In this case, the dynamics of the respective dominant species in this reservoir was a long-term function (>2 years) of the hydrology and hydrodynamics. Long-term changes in the cyanobacterial community structure and a decrease in total cyanobacterial biovolume have also been reported for at least 3 years after several major storm events in a shallow lake, possibly due to persistent high turbidity and turbulent conditions which favoured diatoms and small-celled cyanobacteria over large-celled or filamentous cyanobacteria (James et al., 2008).

Prolonged periods of wind which are related to more intense storms or longer periods of rain were shown to enhance the effect of nutrient input during rainfall by inducing mixing events for up to three months (Bormans et al., 2001 in Shaw et al., 2001). Turbidity can also increase after storm events and it was shown that depending on the strength of the event, the effect might last up to 2 years (James et al., 2008). Also, it has been shown that the intensity of storm events (e.g., cyclones, hurricanes) has increased over the last 30 years (Emanuel, 1987; Webster et al., 2005). Therefore the effect of strong winds on the dynamics of cyanobacterial blooms will play an increasingly important role.

7. Impact of predicted changes in rainfall patterns on the geographic distribution of cyanobacteria

Global warming is responsible for wider geographical distributions of cyanobacterial species. The best known example is the invasion of *Cylindrospermopsis raciborskii*, a tropical and subtropical species, into temperate waterbodies (Padisak, 1997). It has been suggested that this species is able to extend its current distribution due to higher average water and sediment temperatures, and ongoing eutrophication of many waterbodies (Paerl and Huisman, 2009). However the role of changed rainfall patterns on the geographic distribution has so far been largely ignored, probably due to its complex nature. Furthermore, the symptoms of increased temperature and changes in rainfall patterns are often the same, so it is unclear if the effect of rainfall patterns can be separated from the effect of global warming in this discussion. With changing rainfall patterns, the distribution of cyanobacteria can be expected to expand geographically due to longer and more stable

stratification periods and the predicted higher frequency of extreme rainfall events, which both lead to nutrient enrichment and consequently a competitive advantage for cyanobacteria.

8. Overall impact on food webs

The effect of rainfall and changes in rainfall patterns on food webs is a complex interaction of direct and indirect factors. For example, the effect on primary consumers (e.g., zooplankton) will directly depend on the physicochemical changes of the water conditions, and indirectly on the changes in primary producer (i.e. cyanobacteria, phytoplankton) and secondary consumer (e.g., fish) communities and the respective interactions (Fig. 2).

Direct studies on the effect of rainfall on freshwater food webs are scarce. The few that exist indicate that heavy rainfall events lead to higher phytoplankton diversity if events are strong enough to cause flushing and mixing, thus inducing the collapse of a cyanobacterial bloom (Bouvy et al., 1999; Figueredo and Giani, 2001; Jacobsen and Simonsen, 1993). Consequently, this can lead to higher zooplankton biomass if previous blooms consisted of either inedible or toxic but edible cyanobacteria (Jacobsen and Simonsen, 1993), and to weaker trophic interactions (Angeler et al., 2000). However, it was also shown that toxic cyanobacterial blooms can support a high biomass of certain zooplankton genera, such as cyclopoid copepods or rotifers, as they are able to use them as a food source (Bouvy et al., 1999). A relationship between land use, the occurrence of cyanobacteria, and the zooplankton community was found in a study that investigated the effect of forest clearing on lake ecosystems (Ghadouani et al., 2006). A significant decrease of the size structure of zooplankton communities and a shift from large cladocerans to smaller zooplankton, such as copepods, was found after phytoplankton and cyanobacterial biomass increased significantly due to forest harvesting in the catchments of the lakes (Ghadouani et al., 2006).

More conclusions of how changes in rainfall patterns might affect food webs can be derived from general field studies that investigate the effects of cyanobacterial blooms on freshwater ecosystems. Cyanobacterial biomass itself has a significant negative effect on the ecosystem (reviewed in Havens, 2007). For instance, a lower transparency can lead to light limitation of other phytoplankton and macroalgae; high photosynthesis can increase the pH and consequently impact fish populations and alter the interaction between primary producers; the increased food particle size (filamentous or colonial cyanobacteria) may impact grazer communities (Ghadouani et al., 2004, 2003); and a reduced DIC concentration will alter the interaction between primary producers. The collapse of a bloom will lead to anoxia and high ammonium levels that can be potentially responsible for the death of fish and other vertebrates (Havens, 2007). The presence of high cyanobacterial biomass can also lead to phenotypic plasticity (Ghadouani and Pinel-Alloul, 2002), and changes in the behaviour of keystone species such as *Daphnia* which will have consequences for their predators (Reichwaldt, 2008; Reichwaldt and Abrusán, 2007). Therefore, changes in rainfall patterns that affect bloom dynamics will certainly impact

Table 4 – Summary of the predicted effects of likely changes in rainfall patterns on waterbodies, cyanobacterial blooms and ecosystems. ↑ = increase; ↓ = decrease; CB = cyanobacteria; Phyto = non-cyanobacterial phytoplankton; CB > Phyto or Phyto > CB means that conditions favour cyanobacteria or phytoplankton, respectively.

Conditions in waterbody	Possible effects on CB biomass, toxin production and competition between CB and Phyto	Possible mechanisms	Possible consequences for ecosystem
Increased intensity of rainfall event			
Destabilized water column by water inflow and wind	<p><u>Short-term</u> (during mixing conditions)</p> <ul style="list-style-type: none"> • CB biomass ↓ • Toxin production ↓ • Phyto > CB <p><u>Long-term</u> (after mixing conditions)</p> <ul style="list-style-type: none"> • CB biomass ↑ • Toxin production ↑ • CB > Phyto 	<ul style="list-style-type: none"> • Unfavorable for CB due to their relatively slow growth rate^b • Lower toxin production under unfavorable growth conditions^f • Comparatively higher growth rate of other phytoplankton^b • Eutrophication^j by nutrient input from nutrient-rich deep water layer can rapidly be utilized by CB, especially if epilimnion was nutrient limited before^h; re-suspension of CB dormant forms^g • Light limitation under high C, N supply^a • Eutrophication^j 	<p>High diversity system; toxin concentration in the system low</p> <p>Low diversity, species poor system; development of toxic CB blooms; rotifers and calanoid copepods might be dominant</p>
Flushing	<ul style="list-style-type: none"> • CB and Phyto biomass ↓ 	<ul style="list-style-type: none"> • Dilution^e 	<p>Low CB and Phyto biomass levels; toxin concentration in the system low</p>
Nutrient input	<ul style="list-style-type: none"> • CB biomass ↑ • Toxin production ↑ • CB > Phyto 	<ul style="list-style-type: none"> • Eutrophication^j by nutrient input through surface and subsurface flows • Higher toxin production at higher growth rates^{t,b}; higher growth rates of toxic compared to non-toxic strains^o • Eutrophication^j 	<p>Low diversity, species poor system; development of toxic CB blooms; higher biomass carrying capacity of the waterbody; rotifers and calanoid copepods might dominate</p>
Increased turbidity due to sediment re-suspension	<ul style="list-style-type: none"> • CB biomass ↑ • Toxin production ↑ or ↓ • CB > Phyto 	<ul style="list-style-type: none"> • Buoyant CB avoid light limitation by forming surface scum^c; CB can adapt to different light levels^h • ↑: light limitation under high C, N supply^a or ↓: non-toxic strains are better competitors for light under light limitation^p • Relatively higher growth rate of CB under low light intensities^b 	<p>Low diversity, species poor system; development of CB bloom with high or low toxicity; rotifers and calanoid copepods might dominate</p>
Longer dry periods (=lower frequency)			
Lower water level	<ul style="list-style-type: none"> • CB biomass ↑ • Toxin production ↑ or ↓ • CB > Phyto 	<ul style="list-style-type: none"> • Higher temperature increases CB growth rate^b; concentration of nutrients and biomass leads to eutrophication^j and light limitation → CB can adapt to different light levels^h e.g., buoyant CB avoid light limitation by forming surface scum^c • ↑: higher toxin production at higher growth rates^{t, b}; ↓: non-toxic strains are better competitors for light under light limitation^p 	<p>Low diversity, species poor system; development of CB bloom with high or low toxicity; rotifers and calanoid copepods might dominate</p>

Higher water temperature	<ul style="list-style-type: none"> • CB biomass ↑ • Toxin production ↑ • CB > Phyto 	<ul style="list-style-type: none"> • Higher conductivity,ⁱ higher temperature,^b higher turbidity due to biomass^c; eutrophication^j • Higher growth rates at higher temperature^b • Higher toxin production at higher growth rates^b; higher growth rates of toxic compared to non-toxic strains^o • CB outcompete Phyto at higher temperatures^b 	Low diversity, species poor system; development of toxic CB bloom; rotifers and calanoid copepods dominant
Longer water residence time = stable water column (stratification)	<ul style="list-style-type: none"> • CB biomass ↑ • Toxin production ↑ • CB > Phyto 	<ul style="list-style-type: none"> • Nutrient depletion of the euphotic zone, CB have higher affinity to P,N, Fe than Phyto^b; some buoyant CB species migrate to nutrient rich hypolimnion^d • Higher toxin production under growth-favourable conditions^f • Stable conditions favor CB that have lower growth rates than Phyto^{b,h,k} 	Low diversity, species poor system; development of toxic CB bloom; rotifers and calanoid copepods might dominate
Anoxic conditions	<ul style="list-style-type: none"> • CB biomass ↑ • Toxin production ↑ or ↓ 	<ul style="list-style-type: none"> • Nutrients are mobilized from the sediment^l → eutrophication^j • ↑: due to favourable growth conditions^f and increased c(Fe_{sol}),ⁿ ↓: due to increase of c(Fe_{sol})^m 	Low diversity, species poor system; development of CB bloom with high or low toxicity; rotifers and calanoid copepods might dominate
Increased conductivity	<ul style="list-style-type: none"> • CB biomass ↑ or ↓ • Toxin production ↑ or ↓ • CB > Phyto 	<ul style="list-style-type: none"> • Depends on species-specific optimum growth curves • Depends on species-specific optimum growth curves • CB are more salt-tolerant than many Phyto^q 	CB possibly dominant but whether a bloom develops depends on the conductivity level
Rainfall events that end longer dry periods input a disproportionately larger amount of nutrients than rainfall events after shorter dry periods	<ul style="list-style-type: none"> • CB biomass ↑ • Toxin production ↑ • CB > Phyto 	<ul style="list-style-type: none"> • Eutrophication^j • Higher toxin production at higher growth rates^{f, b}; higher growth rates of toxic compared to non-toxic strains^o • Eutrophication^b 	Low diversity, species poor system; development of toxic CB bloom; rotifers and calanoid copepods might dominate
High turbidity due to high biomass	<ul style="list-style-type: none"> • CB biomass ↑ • Toxin production ↑ or ↓ • CB > Phyto 	<ul style="list-style-type: none"> • Buoyant CB avoid light limitation by forming surface scum^c; CB can adapt to different light levels^h • ↑: light limitation under high C, N supply^a or ↓: non-toxic strains are better competitors for light under light limitation^p • Relatively higher growth rate of CB under low light intensities^b 	Low diversity, species poor system; development of CB bloom with high or low toxicity; rotifers and calanoid copepods might dominate
Higher pH due to high photosynthesis levels	<ul style="list-style-type: none"> • CB biomass ↑ or ↓ • Toxin production ↑ or ↓ • CB > Phyto 	<ul style="list-style-type: none"> • Depends on species-specific optimum growth curves • Depends on species-specific optimum growth curves 	CB possibly dominant but it depends on the pH if blooms develop; fish kills due to damaged gills ^b

(continued on next page)

Table 4 – (continued)

Conditions in waterbody	Possible effects on CB biomass, toxin production and competition between CB and Phyto	Possible mechanisms	Possible consequences for ecosystem
		<ul style="list-style-type: none"> • (Buoyant) CB are better competitors at higher pH^d 	
<p>Citations are examples only:</p> <p>a Van de Waal et al., 2009.</p> <p>b Chorus and Bartram, 1999.</p> <p>c Paerl et al., 2011.</p> <p>d Reynolds and Walsby, 1975.</p> <p>e Jones and Poplawski, 1998.</p> <p>f Rivasseau et al., 1998.</p> <p>g Fabbro and Duivenvoorden, 1996.</p> <p>h Shaw et al., 2001.</p> <p>i Orr et al., 2004.</p> <p>j c.f. Prepas and Charette, 2005.</p> <p>k Paerl, 1988.</p> <p>l Chorus and Mur, 1999.</p> <p>m Sevilla et al., 2008.</p> <p>n Utkilen and Gjølme, 1995.</p> <p>o Davis et al., 2009.</p> <p>p Kardinaal et al., 2007.</p> <p>q Tonk et al., 2007.</p>			

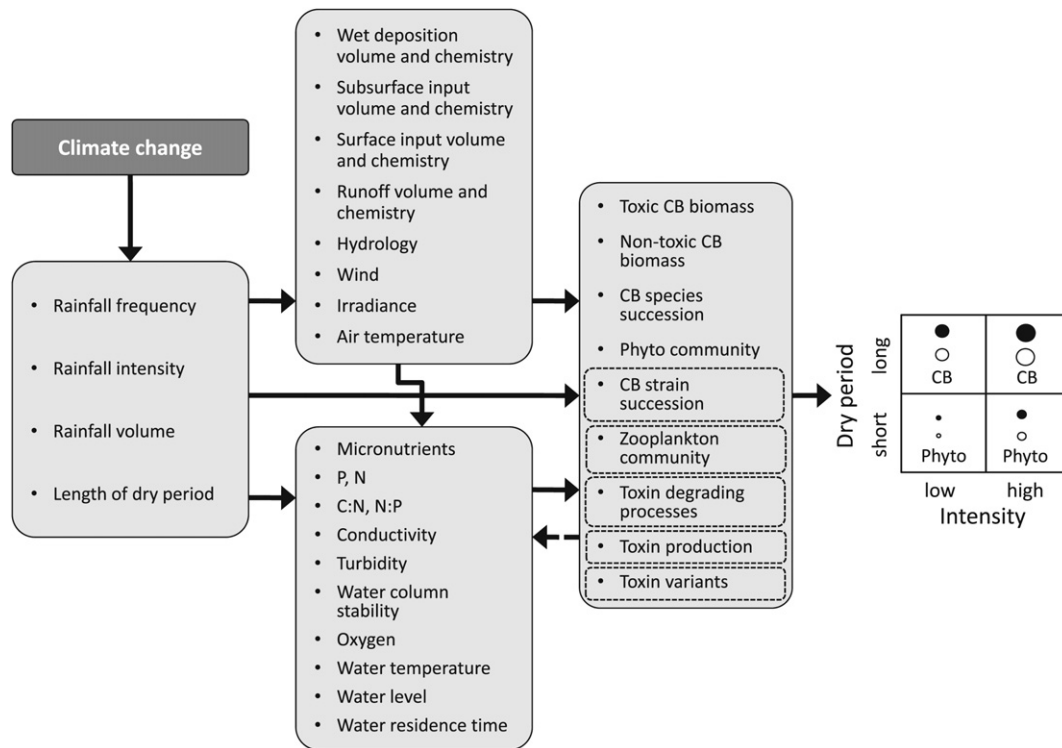


Fig. 4 – Conceptual model identifying the links between climate change, rainfall patterns and toxic cyanobacterial blooms. The framework on the right indicates predictions in terms of cyanobacterial biomass (filled circles) and toxin concentration in the water (open circles) for four different scenarios with regard to rainfall intensity and length of dry periods. The size of the circles represents the relative sequence of the magnitudes for the 4 described scenarios. CB or Phyto indicate the favoured group. Dashed boxes highlight under-researched fields that need special attention.

biodiversity and ecosystems function as well, but this will be a complex function of the direct and indirect effects and of the respective cyanobacterial and zooplankton species.

If blooms also produce toxins, this will additionally affect food web structures as macrophyte, phytoplankton, the microbial loop, zooplankton, macro-invertebrate, and fish populations can be negatively affected through sub-lethal and lethal toxin concentrations (Babica et al., 2006; Havens, 2007; Ibelings and Havens, 2007; Moustaka-Gouni et al., 2006; Zurawell et al., 2005). For instance, cyanobacterial toxins can decrease *Daphnia* grazing on cyanobacteria (Ghadouani et al., 2004) and lead to a decline in *Daphnia* biomass (Ghadouani et al., 2003), and the differential inhibition of population growth of *Daphnia* and rotifers by toxic cyanobacteria can lead to changes in the zooplankton community in favour of rotifers (Smith and Gilbert, 1995). Accumulation of toxins in zooplankton (e.g., Kotak et al., 1996) can also lead to a transfer of the toxin to higher trophic levels (Ibelings and Chorus, 2007; Oberhaus et al., 2007), as toxins have even been found in organisms that do not directly feed on cyanobacteria (Smith and Haney, 2006).

9. Summary

The predicted changes in rainfall patterns (i.e. higher frequency of high intensity rainfall events; longer dry periods) will have a significant impact on the physicochemical conditions of freshwater systems, on cyanobacterial bloom

dynamics, on the toxicity of waterbodies, and on food web structures (Table 4). The impact is very complex and will strongly depend on site-specific dynamics, cyanobacterial species composition, and cyanobacterial strain succession (Fig. 4). The main findings of this review paper can be summarized as the following:

- An increase in the frequency of rainfall events that significantly disturb stratification will diminish cyanobacterial bloom occurrences.
- In the short-term, intense rainfall events can lead to unfavourable conditions for cyanobacteria due to dilution and flushing; in the long term, this effect might often be outweighed by the disproportionately higher nutrient input by increased runoff volume, thus increasing nutrient concentrations and bloom occurrences.
- Long dry-periods (droughts) due to less frequently occurring rainfall events will produce conditions that are favourable for proliferation of many potentially toxic cyanobacterial species (stable water column, warmer water temperature, increased eutrophication).
- A higher number of small rainfall events or wet days can lead to proliferation of cyanobacteria as they can rapidly use nutrients that are added during rainfall events, especially if stratification remains unchanged.
- Toxin concentration in the water can be predicted to increase due to higher carrying capacities supporting higher cyanobacterial biomass, and due to more favourable growth

conditions for cyanobacteria, which will likely increase their toxin production. There is also evidence that input of inorganic nutrients can promote blooms that are dominated by toxic strains. However, the complex interaction of the factors leading to the ultimate toxin concentration in waterbodies is still barely understood, and even less so the impact of rainfall on these interactions; hence any prediction with regard to the toxicity of waterbodies under future scenarios is still very vague.

10. Future challenges

The synthesis in this review highlights that the predicted changes in rainfall patterns will strongly affect the occurrence of toxic cyanobacterial blooms. However, it also stresses the complexity of the dynamics, which makes it hard to predict these effects reliably due to our limited understanding of the mechanisms and their interactions. A lot of our current understanding about cyanobacterial patterns in nature is still derived from laboratory work and we encourage more work that confirms laboratory findings in the field. To be able to sustainably manage our water resources with regard to future cyanobacterial blooms, there are still manifold unknowns that remain to be elucidated. For instance, it is of utmost importance to identify the role of rainfall patterns on the toxin dynamics in waterbodies. This does not only include biomass dynamics of toxic and non-toxic strains but also how rainfall events affect total and variant-specific toxin production and toxin degradation processes (Fig. 4). This is important for assessing the risk for human poisoning and environmental health issues. Understanding the effect of changes in physicochemical parameters on the succession of toxic and non-toxic cyanobacterial species and strains is also essential to be able to assess the effect of climate change on the toxicity of blooms (Fig. 4). Research should also include a wider range of waterbodies. Currently, most studies have focused on artificial drinking reservoirs because maintaining high water quality is important in these systems. However, due to the connectivity of waterbodies, the high risk of poisoning events during recreational activities, and the importance of maintaining lakes and wetlands as important biodiversity spots, additional focus needs to be put on lakes and rivers. Identifying the spatial dynamics of blooms within a system after rainfall events is important to gain a better understanding of the dynamics, which will help to develop more efficient management plans for bloom prevention. Furthermore, the effect of changes in rainfall patterns on food web structures and ecosystem health is very complex and studies should investigate separating direct (physicochemical changes) from indirect (through cyanobacterial blooms) effects. Additionally, these studies should also focus on quantifying the effect of changes in rainfall patterns on higher trophic levels of the food web which will interact and control cyanobacteria. This information will assist in identifying the hazards for ecosystems and developing management strategies. Moreover, with air pollution increasing in large regions of the world, it is important to identify how changes in rainfall chemistry affect bloom dynamics and how important this process will be in the future.

With the anticipated increase of cyanobacterial bloom occurrences, integrated water management strategies are needed to reduce associated costs and to enable sustainable management of the critical resource water (Ghadouani and Coggins, 2011). This includes an evaluation of costs associated with losses of ecosystem services due to changes in rainfall patterns to assess management options. Furthermore, technical developments and applications to decrease cyanobacterial bloom occurrences in a diversity of waterbodies have to be explored (Barrington and Ghadouani, 2008; Barrington et al., 2011; Reichwaldt et al., 2011), and this requires a close collaboration between hydrologists, ecologists, agronomists and economists from various regions of the worlds, emphasising the magnitude of this global problem.

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