



Review

The dual role of nitrogen supply in controlling the growth and toxicity of cyanobacterial blooms



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ARTICLE INFO

Article history:

Received 29 September 2015

Accepted 30 January 2016

Keywords:

Nitrogen
Phosphorus
Cyanobacteria
Microcystis
Diazotrophy
Nutrients

ABSTRACT

Historically, phosphorus (P) has been considered the primary limiting nutrient for phytoplankton assemblages in freshwater ecosystems. This review, supported by new findings from Lake Erie, highlights recent molecular, laboratory, and field evidence that the growth and toxicity of some non-diazotrophic blooms of cyanobacteria can be controlled by nitrogen (N). Cyanobacteria such as *Microcystis* possess physiological adaptations that allow them to dominate low-P surface waters, and in temperate lakes, cyanobacterial densities can be controlled by N availability. Beyond total cyanobacterial biomass, N loading has been shown to selectively promote the abundance of *Microcystis* and *Planktothrix* strains capable of synthesizing microcystins over strains that do not possess this ability. Among strains of cyanobacteria capable of synthesizing the N-rich microcystins, cellular toxin quotas have been found to depend upon exogenous N supplies. Herein, multi-year observations from western Lake Erie are presented demonstrating that microcystin concentrations peak in parallel with inorganic N, but not orthophosphate, concentrations and are significantly lower ($p < 0.01$) during years of reduced inorganic nitrogen loading and concentrations. Collectively, this information underscores the importance of N as well as P in controlling toxic cyanobacteria blooms. Furthermore, it supports the premise that management actions to reduce P in the absence of concurrent restrictions on N loading may not effectively control the growth and/or toxicity of non-diazotrophic toxic cyanobacteria such as the cosmopolitan, toxin-producing genus, *Microcystis*.

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Contents

1. Introduction	88
2. Seasonal cycles in N loading, P loading, and cyanobacterial blooms.	88
3. Bloom-forming, toxic non-diazotrophic cyanobacteria in low P _i waters.	89
4. Evidence for N control of toxic cyanobacteria blooms.	90
5. Exogenous N influences on cellular toxin composition and quotas.	90
6. Intraspecific differences in N influence: toxic versus nontoxic strains	91
7. The dynamics of N, P, <i>Microcystis</i> , and microcystins in western Lake Erie.	92
8. Conclusions and challenges ahead	93
Acknowledgements	94
References	94

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1. Introduction

Toxic cyanobacteria are of worldwide concern because persistent blooms threaten drinking water supplies, recreation, tourism, and fisheries (Chorus and Bartram, 1999; World Health Organization, 2011, and references therein). Such blooms are commonly promoted by excessive nutrient loading (Wetzel, 1983, 2001; Paerl et al., 2011; O'Neill et al., 2012). Thus, there is significant interest in implementing improved management actions to control the nutrients responsible for promoting blooms. The paradigm that primary production in freshwater is controlled by phosphorus (P) (USNAS, 1969; Schindler, 1974) was established decades ago within oligotrophic lakes in Canada (e.g. Dillon and Rigler, 1974; Jones and Bachmann, 1976; Schindler, 1977). It is based largely on the premise that when inorganic nitrogen (N_i) levels are low, diazotrophic or N_2 -fixing cyanobacteria balance ecosystem N deficiencies (Schindler et al., 2008; Schindler, 2012; Scott and McCarthy, 2010). As the total P concentration in many freshwater bodies has increased and total N:P ratios have decreased, a shift has been reported in phytoplankton assemblages toward cyanobacteria dominance (Smith, 1983; Trimbee and Prepas, 1987; Watson et al., 1997).

Over the past several decades, many lakes have been driven increasingly out of stoichiometric balance due to disproportionate anthropogenic inputs of N and P, or management efforts targeting reduction of one nutrient (usually P in freshwaters) but not the other (Conley et al., 2009; Glibert et al., 2011; Burkholder and Glibert, 2013; and references therein). Concurrently, thought has evolved from consideration of only one limiting nutrient to recognition of the importance of ecological stoichiometry in directly and/or indirectly controlling phytoplankton assemblage structure and productivity (Conley et al., 2009; Glibert et al., 2011; Burkholder and Glibert, 2013, and references therein). Consequently, the literature is rich with examples of the importance of P (Schindler, 1977; Wetzel, 2001; Sterner, 2008; and references therein), and N (e.g. Gobler et al., 2007; Davis et al., 2010; Beversdorf et al., 2013, 2015) in controlling cyanobacteria blooms as well as with examples of N and P co-limitation (Elser et al., 1990, 2007; Lewis and Wurtsbaugh, 2008; Xu et al., 2010; Chaffin et al., 2013; Bridgeman and Chaffin, 2013; Davis et al., 2015).

N limitation in freshwater systems has been most commonly reported during warmer months when planktonic cyanobacteria blooms are most common (Gobler et al., 2007; Xu et al., 2010; Chaffin et al., 2013; Bridgeman and Chaffin, 2013; Davis et al., 2015). Although N_2 fixation by cyanobacteria has been thought to minimize the role of N in controlling blooms, various physiological and ecological lines of evidence have indicated that the energetic demands of diazotrophy can restrict the extent to which N_2 fixation can offset N demands and limitation, particularly when concurrent rates of denitrification are considered (Scott and McCarthy, 2010). Moreover, some of the most common toxigenic genera of cyanobacteria, such as *Microcystis* and *Planktothrix* (Chorus and Bartram, 1999; World Health Organization, 2011), are not diazotrophs but, rather, depend on exogenous N supplies for growth and toxin synthesis (Berman and Chava, 1999; Vézic et al., 2002; Davis et al., 2010; Monchamp et al., 2014, and references therein). A strong relationship between the growth of non-diazotrophic cyanobacteria and exogenous dissolved N supplies has commonly been reported. For example, in laboratory studies increased N_i has promoted the growth and toxicity of *Microcystis* (Watanabe and Oishi, 1985; Codd and Poon, 1988; Orr and Jones, 1998) and enhanced input of N_i to systems with elevated P has led to succession from diazotrophs to non-diazotrophs (Bunting et al., 2007; Davis et al., 2010; Chaffin et al., 2013; Harke et al., 2016).

This manuscript reviews recent information regarding the role of N and P in supporting the growth and toxicity of cyanobacteria

blooms, emphasizing non-diazotrophs. Conditions that render ecosystems prone to cyanobacterial blooms are considered, as well as recent molecular, laboratory, and field studies that support the premise that the toxicity, and sometimes the biomass, of cyanobacterial blooms is influenced by N_i availability. Finally, open questions and research priorities are identified toward the goal of strengthening insights regarding nutrient controls on cyanobacterial blooms and toxin production.

2. Seasonal cycles in N loading, P loading, and cyanobacterial blooms

Due to the seasonality of N and P inputs into temperate freshwater ecosystems, late summer cyanobacteria blooms occur when N_i delivery from river sources is often at an annual minimum (Turner et al., 2003) and, thus, most likely to control the growth of primary producers. Similar trends have been observed in smaller lakes more influenced by groundwater flow than riverine input (Gobler et al., 2007). In Lake Erie, which has sustained major cyanobacterial blooms during the past two decades (Brittain et al., 2000; Conroy et al., 2005; Stumpf et al., 2012; Wynne and Stumpf, 2015), one of the dominant nutrient sources, the Maumee River, has an annual TN:TP minimum during the summer months when cyanobacteria blooms are most likely and summer N limitation has been demonstrated (Stow et al., 2015; Chaffin et al., 2013, 2014).

Species and sources of N present in lakes can differ in their seasonal dynamics, which may also influence cyanobacterial blooms. Nitrate concentrations tend to be highest in winter-spring and decline to low levels as summer progresses in many north temperate lakes (Reynolds, 1984; Wetzel, 2001; Chaffin et al., 2011; Bridgeman and Chaffin, 2013). These low N conditions can be alleviated by periodic summer storms that deliver "new" N and/or by diazotrophic cyanobacteria that release ("leak") amino acids and ammonia during N_2 fixation (Wetzel, 2001 and references therein) although nitrogen fixation has been shown to not offset N ecosystem level demands (Scott and McCarthy, 2010).

In contrast to NO_3^- dynamics, ammonia (NH_3) and ionized ammonia (NH_4^+) are released from sediments and some benthic fauna during warmer months through decomposition processes (Wetzel, 2001, and references therein; Zhang et al., 2008). Substantial water-column NH_4^+ supplies from benthic sources in summer have also been reported in areas with moderate to high densities of bivalve molluscs (Burkholder and Shumway, 2011). For example, the western basin of Lake Erie has sustained major invasions of dreissenid mussels capable of delivering large amounts of NH_4^+ to the water column (Higgins et al., 2006, and references therein; Zhang et al., 2008). In lakes showing symptoms of N limitation during late summer, cyanobacteria such as *Microcystis* have been shown to become dominant by rapidly assimilating recycled ammonium (e.g. Takamura et al., 1987; Ferber et al., 2004; Chaffin et al., 2011). Further, *Microcystis* has been shown to have a high affinity for NH_4^+ and, thus, is highly competitive for recycled, reduced N (McCarthy et al., 2009; Glibert et al., 2015, and references therein). Reduced N forms are rapidly recycled; increased loads of reduced N, such as ammonia in partially treated or untreated sewage, and high NH_4^+/NO_3^- ratios, tend to promote cyanobacteria such as *Microcystis* over diatoms in phytoplankton assemblages (McCarthy et al., 2009; Glibert et al., 2015).

Lake sediments and porewaters are generally enriched in inorganic P (P_i) relative to the water column, although the extent to which sediments retain or export these nutrients varies seasonally. The PO_4^{3-} ion binds preferentially with ferric oxides in sediments under oxygenated conditions, but during summer months as temperatures warm and microbial degradation of sedimentary organic matter accelerates, sediment and near-sediment oxygen

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