Review

# Role of toxic and bioactive secondary metabolites in colonization and bloom formation by filamentous cyanobacteria *Planktothrix*

Rainer Kurmayer [a,*], Li Deng [b], Elisabeth Entfellner [a]

[a] University of Innsbruck, Research Institute for Limnology, Mondseestrasse 9, 5310 Mondsee, Austria
[b] Helmholtz Zentrum München, Institute of Groundwater Ecology, Ingolstädter Landstrasse 1, 85764 Neuherberg, Germany

SUMMARY

Bloom-forming cyanobacteria *Planktothrix agardhii* and *P. rubescens* are regularly involved in the occurrence of cyanotoxin in lakes and reservoirs. Besides microcystins (MCs), which inhibit eukaryotic protein phosphatase 1 and 2A, several families of bioactive peptides are produced, thereby resulting in impressive secondary metabolite structural diversity. This review will focus on the current knowledge of the phylogeny, morphology, and ecophysiological adaptations of *Planktothrix* as well as the toxins and bioactive peptides produced. The relatively well studied ecophysiological adaptations (buoyancy, shade tolerance, nutrient storage capacity) can partly explain the invasiveness of this group of cyanobacteria that bloom within short periods (weeks to months). The more recent elucidation of the genetic basis of toxin and bioactive peptide synthesis paved the way for investigating its regulation both in the laboratory using cell cultures as well as under field conditions. The high frequency of several toxin and bioactive peptide synthesis genes observed within *P. agardhii* and *P. rubescens*, but not for other *Planktothrix* species (e.g. *P. pseudagardhii*), suggests a potential functional linkage between bioactive peptide production and the colonization potential and possible dominance in habitats. It is hypothesized that, through toxin and bioactive peptide production, *Planktothrix* act as a niche constructor at the ecosystem scale, possibly resulting in an even higher ability to monopolize resources, positive feedback loops, and resilience under stable environmental conditions. Thus, refocusing harmful algal bloom management by integrating ecological and phylogenetic factors acting on toxin and bioactive peptide synthesis gene distribution and concentrations could increase the predictability of the risks originating from *Planktothrix* blooms.

## Contents

## 1. Phylogeny

The genus *Planktothrix* constitutes one of the early described surface bloom-forming cyanobacteria in freshwater, e.g. references in Staub (1961), although its taxonomic affiliation has undergone continuous revision and refinement. For example, for the longest period of scientific record and documentation, it has been classified under the genus *Oscillatoria* (Gomont, 1892) because it grows in solitary trichomes without sheaths, heterocysts, and akinetes. It has been only since 1988 that the new genus *Planktothrix* has been separated based on its unique ultrastructural characters as well as its life strategy (Anagnostidis and Komárek, 1988). Subsequently, the phylogenetic differentiation of this genus *Planktothrix* from *Oscillatoria* was confirmed by 16S rDNA sequencing (Wilmotte and Herdman, 2001; Suda et al., 2002; Komárek et al., 2014). Currently, the genus *Planktothrix* is validly described under the International Code of Botanical Nomenclature (ICBN) (Anagnostidis and Komárek, 1988; Gaget et al., 2015), while an attempt to validate the genus name under the International Code of Nomenclature of Prokaryotes (ICNP) failed (Suda et al., 2002; Oren, 2004). More than 25 years ago, in 1989, Castenholz & Waterbury (Oren, 2004) concluded that, in the foreseeable future, the two classification systems (ICBN and ICNP) of cyanobacteria will (co-)exist. This pragmatic solution has been maintained and in the current taxonomy, the polyphasic approach including genetic, physiological, cell-structural, etc., information is routinely applied, e.g. Gaget et al. (2015). Suda et al. (2002) revised water-bloom-forming species of oscillatorioid cyanobacteria and defined three phylogenetic groups: (I) *P. agardhii* (Gomont) Anagnostidis et Komárek 1988 and *P. rubescens* (DeCandolle ex Gomont) Anagnostidis et Komárek 1988, (II) *P. pseudagardhii* Suda et Watanabe, (III) *P. mougeotii* (Kützing ex Lemmermann) (Bory ex Gomont) Anagnostidis et Komárek 1988. This phylogenetic assignment has been emended by Liu et al. (2013) describing *P. spiroides* Wang et Li 2013 from strains isolated from freshwater in China. Recently, Gaget et al. (2015) described three new *Planktothrix* species: *P. paucivesiculata* Gaget et al., *P. tepida* Gaget et al., *P. serta* Gaget et al. using the polyphasic approach.

## 2. Morphology

Filamentous cyanobacteria like *Planktothrix* are formed by the binary division of cells in one plane at right angles to the long axis, while the cells remain attached to each other with little or no constriction at the cross-walls. Typically, the cells are cylindrical, a little shorter than wide, and the trichomes are solitary, straight, or slightly curved. Those filaments may contain hundreds to thousands of cells, and the trichomes are a few micrometers in diameter. The length of the filaments varies, while some species (*P. rubescens*) grow in filaments up to a few millimeters in length. The filaments may be attenuated toward the ends or terminal cells of a trichome may be tapered, with or without a cap (calyptra). Currently, nine *Planktothrix* morphospecies are differentiated and categorized into three groups (Komárek and Anagnostidis, 2007): (1) morphospecies forming wavy and coiled filaments (*P. cryptovaginata* (Skorbatov) Anagnostidis et Komárek 1988, *P. planctonica* (Elenkin) Anagnostidis et Komárek 1988); (2) morphospecies forming rather straight filaments, not attenuated and lacking a cap (*P. isothrix* (Skuja) Komárek et Komarkova 2004, *P. compressa* (Utermöhl) Anagnostidis et Komárek 1988, *P. clathrata* (Skuja) Anagnostidis et Komárek 1988, *P. suspensa* (Pringsheim) Anagnostidis et Komárek 1988; and (3) attenuated filaments with tapering toward the ends sometimes showing a calyptra (*P. agardhii* (Gomont) Anagnostidis et Komárek 1988, *P. rubescens* (DeCandolle ex Gomont) Anagnostidis et Komárek 1988, *P. prolifica* ([Greville] Gomont) Anagnostidis et Komárek 1988).

To a certain extent, there is correspondence between the morphospecies concept (Anagnostidis and Komárek, 1988) and the polyphasic approach introduced by Suda et al. (2002). For example, the *P. agardhii* and *P. rubescens* group (*sensu* Suda et al., 2002) is similarly differentiated by the morphospecies concept. The species *P. mougeotii* (*sensu* Suda et al., 2002) might correspond with *P. isothrix* (Skuja) Komárek et Komarkova 2004 (Table 1). In contrast *P. pseudagardhii* (*sensu* Suda et al., 2002) cannot be differentiated by morphological characters only. Several species of the polyphasic taxonomy approach fit to different morphospecies (e.g. *P. mougeotii* vs. *P. isothrix* or *P. compressa* and *P. clathrata*). In the near future, it seems possible to merge the polyphasic taxonomy system with the morphospecies concept, not least because the genus *Planktothrix* is amenable to isolation following standard microbiological techniques (Rippka 1988), and a number of collections with clonal isolates are available: e.g. NIVA-CCA, Norwegian Institute for Water Research, Culture Collection of Algae, https://niva-cca.no/; PCC, Biological Resource Center of Institute Pasteur (CRBIP)-Pasteur Culture Collection of Cyanobacteria, http://cyanobacteria.web.pasteur.fr/; SAG, Culture Collection of Algae at Göttingen University, http://www.uni-goettingen.de/en/about-sag/184983.html; NIES-MCC, National Institute of Environmental Studies, Microbial Culture collection, http://mcc.nies.go.jp/; CCAP, Culture Collection of Algae and Protozoa, http://www.ccap.ac.uk/; CPCC, Canadian Phycological Culture Centre, https://uwaterloo.ca/canadian-phycological-culture-centre. It is noted that *Planktothrix* isolates from benthic habitats have been reported, which seem to be most closely related to *P. mougeotii* (Wood et al., 2010). From various habitats, however, *P. agardhii* and *P. rubescens* are most commonly isolated and characterized and, therefore, will be focused on in the following sections.

## 3. Ecophysiological adaptations

Within the genus *Planktothrix*, it is frequently *P. agardhii* and *P. rubescens* that dominate the phytoplankton in the water column. Understanding the ecophysiological adaptations helps to explain the competitiveness and invasive ability of *Planktothrix*.

### 3.1. Buoyancy

The most successful way to overcome the tendency to sink out of the euphotic zone is to maintain a gas-filled space within the protoplast — a gas vesicle has a density of approx. one tenth that of water and thus gives the cells a lower density (Walsby, 1994). Due to the generation of polysaccharides via photosynthesis, the cellular weight increases and, due to respiration processes, the cellular weight decreases (Reynolds et al., 1987). Changes in cellular weight can be balanced via gas vesicles leading to optimal physiological conditions for the organism either on the surface or at a certain depth in the water column (Konopka et al., 1993).