WATER RESEARCH 66 (2014) 320–337

Available online at www.sciencedirect.com

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Review

In search of environmental role of cylindrospermopsin: A review on global distribution and ecology of its producers

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ARTICLE INFO

Article history:
Received 14 May 2014
Received in revised form
20 August 2014
Accepted 21 August 2014
Available online 3 September 2014

Keywords:
Cylindrospermopsin
Cylindrospermopsis raciborskii
Ecological role
Grazers defence
Allelopathy

ABSTRACT

Despite a significant interest in cyanotoxins over recent decades, their biological role is still poorly elucidated. Cylindrospermopsin (CYN) is a cyanobacterial metabolite that is globally identified in surface fresh- and brackish waters and whose producers are observed to spread throughout different climate zones. This paper provides a comprehensive review of the characteristics and global distribution of CYN-producing species, the variety of their chemotypes and the occurrence of strains which, while incapable of toxin synthesis, are able to produce other bioactive compounds including those that are hitherto unknown and yet to be identified. Environmental conditions that can trigger CYN production and promote growth of CYN-producers in aquatic ecosystems are also discussed. Finally, on the basis of existing experimental evidence, potential ecological role(s) of CYN are indicated. It is eventually concluded that CYN can be at least partially responsible for the ecological success of certain cyanobacteria species.

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http://dx.doi.org/10.1016/j.watres.2014.08.029
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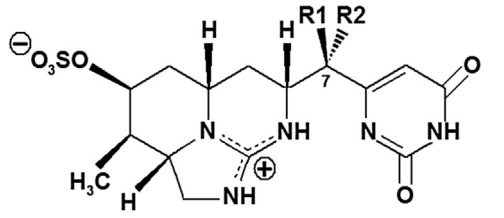
1. Introduction

Cylindrospermopsin (CYN), a cyanobacterial metabolite, has been the object of great scientific interest since its chemical structure was proposed for the first time in 1992 (Ohtani et al., 1992). CYN ($C_{15}H_{21}N_5O_7S$) is a highly water soluble polyketide-derived alkaloid with a central functional guanidino moiety combined with hydroxymethyluracil attached to its tricyclic carbon skeleton (Fig. 1). The occurrence of natural analogs of 7-epi-CYN (an epimer at the hydroxyl bridge) and 7-deoxy-CYN (lacking the hydroxyl group) has also been recently reported (Banker et al., 2001; Seifert et al., 2007). CYN was identified in some reservoirs used for supplying drinking water (Bittencourt-Oliveira et al., 2014; Lei et al., 2014) and has been documented as being involved in at least two epidemical cases of human poisoning (Carmichael et al., 2001; Griffiths and Saker, 2003). Moreover, a broad range of experimental *in vivo* and *in vitro* studies focusing on CYN toxicity in mammalian cells have been undertaken (reviewed by Poniedziałek et al., 2012; de la Cruz et al., 2013). CYN has been shown to interfere with different metabolic pathways (Runnegar et al., 1995; Froscio et al., 2003) and induce a wide range of responses including oxidative stress (Gutiérrez-Praena et al., 2012), genotoxicity (Humpage et al., 2000; Žegura et al., 2011), immunosuppresion (Poniedziałek et al., 2014a,b) and abnormal function of hepatocytes (Chong et al., 2002). While investigations of the toxic mechanism of CYN action along with systematic monitoring of surface waters are necessary for proper risk assessment and the protection of human health, they do not answer the fundamental questions as to the factual biological role of this cyanobacterial compound. This, however, is crucial in understanding the dynamics of CYN production and the occurrence of CYN-producers, which are currently observed essentially in encompassing tropical, subtropical and temperate climate zones.

Over the past several centuries, spread of cyanobacteria in surface waters and increased incidence of cyanobacterial blooms has been observed. As recently indicated by Sukenik et al. (2012), also species capable of CYN biosynthesis are expected to maintain their presence in new habitats and further expand to new environments. This hypothesis is partially supported by the increased incidence of the first recognized CYN-producer, *Cylindrospermopsis raciborskii* over recent decades, especially in temperate zones (Sinha et al., 2012). Several explanations of this phenomenon have been suggested and include: high phenotypic plasticity (Bonilla et al., 2012), climate changes (Paerl and Paul, 2012) and cultural eutrophication (O'Neil et al., 2012).



	R1	R2
CYN	OH	H
7-deoxy CYN	H	H
7-epi CYN	H	OH

Fig. 1 – Chemical structure of cylindrospermopsin and two natural analogs.

The biological and ecological role of cyanotoxins such as CYN and others (e.g. microcystins, nodularins, saxitoxins and anatoxins), has so far been rarely addressed and, as yet, poorly elucidated (Kaplan et al., 2012). Because cyanobacteria represent one of the oldest and morphologically most highly diversified group of prokaryotes (Schirrmeister et al., 2011), it can be speculated that biosynthesis of cyanotoxins such as CYN can be a part of their long-term evolutionary adaptation to the inhabited environment. Surprisingly, the natural occurrence of strains (hereafter non-CYN-producing) lacking genes specific for CYN synthesis and consequently unable to produce this metabolite has recently been reported (Fathalli et al., 2011; Kokociński et al., 2013). This, on the other hand, raises another intriguing question as to the evolutionary reasons behind losing CYN-production potencies (or never acquiring them) and the environmental factors that are behind this loss (or no acquisition).

This paper discusses the global distribution of CYN-producing cyanobacteria species as well as the potential environmental factors that trigger the biosynthesis of this compound. Considering available data, we also indicate broadly the possible biological role(s) of CYN and its implication in the ecological success of toxin producers. Finally, we raise several questions and unresolved issues which, if addressed in future research, may help achieve an understanding of the biological role of this emerging metabolite as well as the diversity and distribution of its producers.

2. CYN producers: global distribution and chemotypes

CYN-producing cyanobacteria are represented by filamentous species belonging to *Nostocales* and *Oscillatoriales* orders. To date, thirteen species have been reported as potent producers of this alkaloid: *C. raciborskii* (Ohtani et al., 1992), *Aphanizomenon ovalisporum* (Banker et al., 1997), *Aphanizomenon flos-aquae* (Preußel et al., 2006), *Aphanizomenon gracile* (Rücker et al., 2007; Kokociński et al., 2013), *Aphanizomenon klebahnii* (Bláhová et al., 2008), *Umezakia natans* (Harada et al., 1994), *Raphidiopsis curvata* (Li et al., 2001a), *Raphidiopsis mediterranea* (McGregor et al., 2011), *Anabaena bergii* (Schembri et al., 2001), *Anabaena planctonica* (Brient et al., 2009), *Anabaena lapponica* (Spoof et al., 2006), *Lyngbya wollei* (Seifert et al., 2007) and at least several

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