Harmful Algae 54 (2016) 44–53

Contents lists available at ScienceDirect

Harmful Algae

journal homepage: www.elsevier.com/locate/hal

Review

Understanding the winning strategies used by the bloom-forming cyanobacterium *Cylindrospermopsis raciborskii*

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A R T I C L E I N F O

Article history:
Received 12 May 2015
Accepted 14 October 2015

Keywords:
Cylindrospermopsin
Saxitoxin
Nutrients
Light
Carbon dioxide
Phytoplankton

A B S T R A C T

The cyanobacterium *Cylindrospermopsis raciborskii* is a widespread species increasingly being recorded in freshwater systems around the world. It is of particular concern because strains in some geographic areas are capable of producing toxins with implications for human and animal health. Studies of this species have increased rapidly in the last two decades, especially in the southern hemisphere where toxic strains are prevalent. A clearer picture is emerging of the strategies adopted by this species to bloom and out-compete other species. This species has a high level of flexibility with respect to light and nutrients, with higher temperatures and carbon dioxide also promoting growth. There are two types of toxins produced by *C. raciborskii:* cylindrospermopsins (CYNs) and saxitoxins (STXs). The toxins CYNs are constitutively produced irrespective of environmental conditions and the ecological or physiological role is unclear, while STXs appear to serve as protection against high salinity and/or water hardness. It is also apparent that strains of this species can vary substantially in their physiological responses to environmental conditions, including CYNs production, and this may explain discrepancies in findings from studies in different geographical areas. The combination of a flexible strategy with respect to environmental conditions, and variability in strain response makes it a challenging species to manage. Our ability to improve bloom prediction will rely on a more detailed understanding of the complex physiology of this species.

Contents

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http://dx.doi.org/10.1016/j.hal.2015.10.012
1568-9883/

1. Introduction

The freshwater filamentous cyanobacterium, *Cylindrospermopsis raciborskii* (Wołoszyńska) Seenayya and Subba Raju is a widespread species. It is increasingly being recorded as present or in bloom proportions in lakes, reservoirs and rivers throughout the world (Padisák, 1997; Sinha et al., 2012). It is of particular concern in countries where it produces toxins. It was first deemed a harmful bloom species after a toxic bloom event in 1979 (Hawkins et al., 1985). There were 148 casualties including 10 adults and 138 children presenting with a range of severe symptoms including anorexia, vomiting and tender hepatomegaly. The structure of cylindrospermosins (CYNs), the toxins responsible, was determined by Ohtani et al. (1992). It is now well established that CYNs are also produced by some New Zealand (Wood and Stirling, 2003) and Asian strains (Li et al., 2001; Wimmer et al., 2014). Later, researchers found that South American strains produce saxitoxins (STXs) (Lagos et al., 1999; Neilan et al., 2003).

Previous reviews have highlighted characteristics of this species that have contributed to its success globally (e.g. Burford and Davis, 2011; O'Neil et al., 2012; Sinha et al., 2012). In particular, studies have shown that it has the ability to alternate nitrogen fixation and dissolved nitrogen uptake, and can utilise and store phosphorus very efficiently (Sprőber et al., 2003; Burford et al., 2006; Isvánovics et al., 2000). It is also adapted to low light conditions and can regulate its buoyancy (Kehoe, 2010). Additionally, this species can grow at a wide range of temperatures, although it prefers summer temperatures in temperate and subtropical areas, while in the tropics it can bloom year-round (e.g. Briand et al., 2004; Chonudomkul et al., 2004; Soares et al., 2013a).

There has been considerable interest in *Cylindrospermopsis raciborskii* in recent years with the number of scientific publications and reviews increasing rapidly (e.g. O'Neil et al., 2012; Sinha et al., 2012). Therefore, this review focuses on the most recent studies into the biogeography, toxins, physiology and ecology of this species, and synthesises this knowledge to provide key new insights into strategies used by this species for competitive success.

2. Biogeography

The cyanobacterium *Cylindrospermopsis raciborskii* is a diazotrophic and filamentous with terminal heterocytes, belonging to the order Nostocales. It was initially described as *Anabaena raciborskii* by Wołoszyńska (1912) in a sample from Java. Initial observations were restricted to the Indo-Malayan region, and subsequent records indicated a "pantropical" distribution. We now know, however, that *C. raciborskii* is found in many tropical/subtropical regions of the world including Australia (Harris and Baxter, 1996; Saker et al., 1999; McGregor and Fabbro, 2000), Thailand (Li et al., 2001), South America (Figueredo and Giani, 2009) and Africa (Mohamed, 2007; Haande et al., 2008). Scientific evidence for its occurrence in temperate regions, such as Europe and North America, is more recent (Briand et al., 2004; Moreira et al., 2011). The increasing number of reports of *C. raciborskii* in temperate regions of the world suggests that the organism could be expanding its geographical range. Despite this, it is difficult to ascertain whether this is due to increased monitoring or true invasiveness of the species.

Several theories have been proffered for the invasiveness of *Cylindrospermopsis raciborskii*. Padisák (1997) attributed the spread from tropical/subtropical zones to temperate zones to two main evolutionary centres. *C. raciborskii* acquired several adaptation mechanisms at these evolutionary centres that have aided its survival outside its original native range, thereby giving it a competitive edge over other phytoplankton species. These physiological adaptations include akinete formation and a tolerance to low phosphorus and nitrogen availability. This combination of physiological adaptations together aids survival in unfavourable conditions. In addition, the existence of multiple ecotypes (Piccini et al., 2011) and the noteworthy phenotypic plasticity (Bonilla et al., 2012) are key factors allowing this species to inhabit a wide range of environments globally.

African lakes have been suggested as the primary geographic origin for the evolution of *Cylindrospermopsis raciborskii* (Padisák, 1997). This is attributed to the occurrence of a high diversity of strains within the species at this location. Thus, it was suggested that *C. raciborskii* adapted to the lower nitrogen and phosphorus conditions in African lakes and then dispersed to tropical regions of Central America and Indonesia. Australia has been suggested as the secondary centre for the evolution of *C. raciborskii* (Padisák, 1997). Many rivers in Australia exhibit high flow variability that results in periodic drying and hence salinity flux (Walker et al., 1995). Thus, Padisák (1997) hypothesised that the salinity tolerance of *C. raciborskii* evolved in this environment.

Expansion of *Cylindrospermopsis raciborskii* has continued in recent times, with Antarctica being the only continent without records of its occurrence (O'Neil et al., 2012; Sukenik et al., 2012). There is evidence that eutrophication and global climate change have also favoured this species in recent decades (Carey et al., 2012; Sinha et al., 2012). Certainly, studies have demonstrated a link between increasing temperatures and earlier springtime initiation of growth (Wiedner et al., 2007). It is likely that different selective pressures in these diverse environments directed these tertiary centres of evolution of *C. raciborskii* 'toxitypes'. Anthropogenic factors, such as dispersal through the ballast of ships, or inappropriate transfer of scientific samples, and dispersal by birds have also been suggested as potential mechanisms contributing to the spread of *C. raciborskii* (Padisák, 1997; Moreira et al., 2011).

Gugger et al. (2005) proffered an alternative hypothesis for the current geographical distribution. They suggested that extinction of *Cylindrospermopsis raciborskii* occurred during the Pleistocene in most geographical locations, and advocated its survival only in warmer climatic conditions on each continent, excluding Antarctica (Gugger and Hoffmann, 2004). Increasing temperatures within the temperate zones has since allowed recolonisation and favoured further spread of the species on the European and the American continents. To further support the distribution of specific *C. raciborskii* genotypes, strains lacking the CYNs synthesis gene cluster, i.e. *cyr* from New Zealand, were shown to have an ancient phylogenetic relationship with those from South America, distinct