Autecology of *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya et Subba Raju

Autecologia de *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya et Subba Raju

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Abstract: Aim: *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya and Subba Raju, also called *Raphidiopsis raciborskii*, is a diazotrophic and filamentous cyanobacterium with terminal heterocytes, belonging to the order Nostocales. It has been the focus of several studies due to its toxicity and wide geographic distribution. **Methods:** To understand its autecology and to identify the key factors that control its dominance, the present review discusses, based on recent publications, whether the expansion of this species is a result of a high metabolic plasticity or the existence of distinct ecotypes. **Results:** Among the factors influencing *C. raciborskii* growth are its ability to survive in wide temperature, light intensity and pH ranges; to dominate in both stratified and mixed environments; to tolerate oligohaline conditions; to produce and secrete allelopathic substances; suffer little herbivore pressure; and although associated with a eutrophic environment, to tolerate low concentration of phosphorus and nitrogen with a high affinity for ammonia. **Conclusions:** Due to these differences in the environmental conditions of growth and development found in various studies, we suggest the existence of different ecotypes that will predominate under specific environmental conditions as the most appropriate hypothesis.

Keywords: Nostocales; metabolic plasticity; ecotypes; environmental factors.

Resumo: Objetivo: *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya e Subba Raju, também chamada de *Raphidiopsis raciborskii*, é uma cianobactéria diazotrófica e filamentosa com heterócitos terminais, pertencente à ordem Nostocales, que tem sido foco de vários estudos por conta da sua toxicidade e ampla distribuição geográfica. **Métodos:** Para compreender a sua autoecologia e identificar os fatores-chave que controlam sua dominância, a presente revisão discute, com base em publicações recentes, se a expansão dessa espécie é resultado de uma elevada plasticidade metabólica ou a existência de ecótipos distintos. **Resultados:** Dentre os principais fatores ambientais sobre o crescimento de *C. raciborskii* estão sua capacidade de sobreviver em um amplo intervalo de temperatura, intensidade luminosa e pH, dominar tanto em ambientes estratificados quanto misturados, preferir condições oligohalinas, produzir e secretar substâncias alelopáticas, sofrer pequena pressão de herbivoria, e, apesar de associada a ambiente eutróficos, tolerar baixa concentração de fósforo e de nitrogênio

com alta afinidade a amônio **Conclusões:** Devido a estas diferenças significativas relacionadas às condições ambientais de crescimento e desenvolvimento apontadas nos diversos estudos, sugerimos como hipótese mais apropriada a existência de diferentes ecótipos que predominarão em condições ambientais específicas.

Palavras-chave: Nostocales; plasticidade metabólica; ecótipos; fatores ambientais.

1. Introduction

Cylindrospermopsis (or *Raphidiopsis*) is a cyanobacterial genus belonging to the order Nostocales and the family Nostocaceae, found in the planktic community of continental waters (Hauer & Komárek, 2019). The most widely distributed species of the genus is *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya and Subba Raju (Alster et al., 2010; Wojciechowski, 2013).

Recent studies using molecular methods (Li et al., 2017; Aguilera et al., 2018; Abreu et al., 2018; Duval et al., 2018; Fuentes-Valdés et al., 2018; Xie et al., 2018) have demonstrated the genetic similarity between the *Cylindrospermopsis* and *Raphidiopsis* genera: a finding that would justify the terms being used synonymously, with temporal prerogative given to the latter. Accepting this taxonomic evidence, the species *Cylindrospermopsis raciborskii* would be called *Raphidiopsis raciborskii*. However, in this work we use *C. raciborskii* as it is the best-known name for the species.

This species is characterized by presenting isopolar trichomes – solitary, spiral or straight, cylindrical cells with slight attenuation towards the ends, and little or no constriction at the cross walls. They form terminal heterocytes with akinetes located internally within the trichomes (Alster et al., 2010; Komarek, 2013; Wojciechowski et al., 2016; Guiry & Guiry, 2019; Hauer & Komárek, 2019). Reproduction is by fragmentation of the trichome or by akinete formation.

In the last decade, *C. raciborskii* has received remarkable attention because of its ability to form blooms, which, in turn, can result in ecological and public health problems in aquatic ecosystems (Leonard & Paerl, 2005; Willis et al., 2017), by changing the water quality through the production of different cyanotoxins (Hawkins et al., 1997; Padisák & Reynolds, 2003; Vehovszky et al., 2015).

According to Wojciechowski et al. (2016) and Zhang et al. (2014), toxin production varies among strains, and the production of two alkaloid variants has been recorded so far in Brazil. Cylindrospermopsin (CYN) (Wiedner et al., 2007; Hoff-Risseti et al., 2013; Babanazarova et al., 2015; Noyma et al., 2015; Vehovszky et al., 2015; Willis et al., 2015; Burford et al., 2016) and saxitoxin (STX) (Alster et al., 2010; Hoff-Risseti et al., 2013; Lopes et al., 2015; Beamud et al., 2016; Burford et al., 2016) are produced by *C. raciborskii*, but in distinct lineages (Hawkins et al., 1985; Lagos et al., 1999). Both cyanotoxins are considered a potential risk to human health. CYN has been shown to cause cell necrosis and lesions, especially in the liver, kidneys, thymus and heart of vertebrates (Humpage et al., 2000; Froscio et al., 2003;), and SXT acts as a neurotoxin that affects the propagation of nerve impulses, resulting in neuromuscular paralysis (Wang et al., 2003; Su et al., 2004).

Although the physiological ecology of *C. raciborskii* has been studied extensively, several aspects have only recently been investigated. These include the distribution and dispersion of the species (Padisák, 1997; Alster et al., 2010; Bolius et al., 2017; Weithoff et al., 2017), the number and size of akinetes (Padisák, 2003), and the causes of toxin production (Babanazarova et al., 2015; Beamud et al., 2016; Burford et al., 2016; Casali et al., 2017).

Hoff-Risseti et al. (2013) suggested a shift over time in the type of cyanotoxins produced by South American strains of *C. raciborskii*. This is supported by the presence of SXT and CYN genes identified and sequenced from the Brazilian planktonic *C. raciborskii* strains CENA302, CENA303, CENA305 and T3.

This paper is a review of the most recent publications regarding *C. raciborskii* occurring in natural environments and lab conditions. We aim to discuss if the wide distribution of *C. raciborskii* is the result of high metabolic plasticity or the existence of different ecotypes. This understanding may have implications for control measures for this species and will summarize knowledge about its function in aquatic ecosystems.

2. Geographical Distribution and Environmental Requirements of *C. raciborskii*

According to Padisák (1997), *C. raciborskii* is widely distributed throughout the Earth. Its presence in varied environments, such as oligotrophic reservoirs, shallow and hypereutrophic lakes, rivers, and other environments with high

water flow, has been increasingly reported (Maia-Barbosa et al., 2010; Bittencourt-Oliveira et al., 2012; Kokociński & Soininen, 2012; Medeiros et al., 2015; Willis et al., 2017; Rzymski et al., 2018; Walter et al., 2018).

Cylindrospermopsis raciborskii has been recorded in tropical and subtropical regions of Africa, Australia, Cuba, India, Indonesia, Oceania and South America. The species is also found in temperate regions of Europe, Central Asia and North America. It forms extensive toxic proliferations in water bodies throughout the world, except in Antarctica (Padisák, 1997, 2003; Wiedner et al., 2007; Antunes et al., 2015). Palmer (1969) reported the first occurrence of this species in Brazil, and its blooms have subsequently been recorded in several Brazilian reservoirs (Branco & Senna, 1994; Souza et al., 1998, Bouvy et al., 1999, 2000; Molica et al., 2002; Tucci & Sant'Anna, 2003; Gemelgo et al., 2008; Figueredo & Giani, 2009; Gomes et al., 2013; Casali et al., 2017).

The success of *C. raciborskii* in aquatic environments worldwide is attributed to its tolerance to broad ranges of various environmental factors (discussed below). To date, the factors most strongly suggested as contributors to flowering and expansion of Cyanobacteria blooms, including *C. raciborskii*, are eutrophication (Soranno, 1997; Paerl, 1997; Saker & Griffiths, 2001; Landsberg, 2002; Huisman & Hulot, 2005;) and climate change (Peperzak, 2003; Paerl & Huisman, 2008; Paul, 2008; Sinha et al., 2012; Kokociński et al., 2017; Panou et al., 2018).

3. Abiotic Factors

Studies of phytoplankton communities have traditionally begun with a survey of the abiotic factors that influence the growth of a given species, in order to then identify determining or influencing factors at the population-level. Following this approach, this work will discuss a number of abiotic factors including light, temperature, pH, nutrients and thermal stability of the water column, in order to understand the growth and predominance of *C. raciborskii* in aquatic environments.

3.1. Temperature

In temperate climates, *C. raciborskii* has been observed at maximum temperature of 35ºC and minimum temperature of 11 °C, with variation among countries: Portugal (11 °C to 35 °C; Saker et al., 2003; Antunes et al., 2015), Australia (19.1 °C to 32 °C; Everson et al., 2011;

Recknagel et al., 2014; Kehoe et al., 2015), France (14.1 °C to 25.7 °C; Briand et al., 2002), Switzerland (≤ 12 °C; Dokulil, 2016), Finland (19 °C to 20 °C; Engstrom-Ost et al., 2015), southern Canada (22 °C to 24 °C; Hamilton et al., 2005), and Hungary, Netherlands and Argentina (11 °C to 20 °C; Bonilla et al., 2012). These data indicate that *C. raciborskii* proliferation occurs, regardless of the season, but that growth and dominance is favored out of the winter period in temperate climates (when the temperature falls below 8 °C). Due to the wide distribution at different temperatures, Chonudomkul et al. (2004) concluded that the expansion of this species in temperate climates may result from the selection of clones with different requirements.

The water temperature in subtropical climates, where this species dominates, ranges from 11.2 °C to 35 °C. Fabre et al. (2010) and Bonilla et al. (2012) observed *Cylindrospermopsis raciborskii* at temperatures of 11.2 °C to 19 °C in Uruguay; Chonudomkul et al. (2004) at 15 °C to 35 °C, in Thailand and southern Japan; Fuentes et al. (2010) above 25 °C, in Louisiana; Jones & Sauter (2005) at 18.2 °C to 26.5 °C, in Indiana; and Thomas & Litchman (2016) at 20 °C to 33 °C, in Florida. Therefore, *C. raciborskii* was not observed only during the winter, when temperatures can reach 0 °C.

The temperature in tropical climates, where this cyanobacterium dominates, varied from 13 °C to 35 °C. Berger et al. (2006) and Dufour et al. (2006) observed a temperature range from 20 °C to 35 °C, in Senegal, Africa; Bouvy et al. (1999), Bouvy et al. (2000), and Bittencourt-Oliveira et al. (2011) from 21.6 °C to 23 °C in the rainy season (summer) and from 23.1 °C to 29.1 °C in the dry season in Pernambuco State, Brazil; Maia-Barbosa et al. (2010) and Figueredo et al. (2014) from 20 °C to 35 °C, in Minas Gerais State, Brazil; Souza et al. (1998), Tucci & Sant'Anna (2003), Gemelgo et al. (2008) and Bonilla et al. (2012) from 13 °C to 28 °C in São Paulo State, Brazil; Soares et al. (2013) from 12 °C to 32 °C in Rio de Janeiro State, Brazil; and Casali et al. (2017) observed a temperature range of 16.8 to 21.8 °C in a mesotrophic subtropical reservoir dominated by *C. raciborskii*, in São Paulo, Brazil.

Proliferations of the species have never been observed in polar climates (Padisák, 1997), corroborating the statements made by Chonudomkul et al. (2004), Mehnert et al. (2010) and Engström-Öst et al. (2015), that *C. raciborskii* does not dominate at temperatures below 10 °C.

According to Recknagel et al. (2019), *C. raciborskii* growth is directly related to

high temperatures (> 24 °C) in temperate and Mediterranean environments and poorly correlated to them in tropical and subtropical environments.

According to a laboratory study by Xiao et al. (2017), *Cylindrospermopsis raciborskii* cells become smaller under higher temperatures. On the other hand, under lower temperatures, the cells become larger with a lower cell concentration. In addition, Bonilla et al. (2016) argued that temperature-derived effects, such as the mixing of regime changes, were the factors that affected the distribution of the species, rather than temperature itself.

Thus, regardless the region and climate, this species can dominate in a wide temperature range from 11 °C to 35 °C. These temperatures are found in most aquatic environments in temperate, subtropical and tropical regions. However, several studies indicate that temperature 2increasing in temperate regions is one of the causes of invasion of European aquatic environments by this species (Bonilla et al., 2012; Recknagel et al., 2019; Kokocinski et al., 2017).

3.2. Light

Padisák (1997), Burford & Davis (2011), Engström-Öst et al., 2015 and Beamud et al. (2016) argued that *Cylindrospermopsis raciborskii* is tolerant to low light intensity as it does not require intense radiation to grow. Furthermore, it has a wide shade tolerance due to chromatic adaptation and the ability to increase the concentration of phycobiliproteins, widening the spectrum of light it can absorb. Because of this shade tolerance, it has an increased competitiveness in highly turbid waters, supporting an ability to grow with little underwater light (Brasil et al. 2017; Engström-Öst et al., 2015).

Yamamoto & Shiah (2012), Bonilla et al. (2012) and Noyma et al. (2015) suggested that the adaptation of *C. raciborskii* to a wide range of irradiance is one of its most important ecological advantages and could have facilitated its dominance. In laboratory conditions, the saturating irradiance (Ik), defined as the ratio of light-saturated growth rate to the initial slope of de growth versus irradiance curve, ranges from 8.5 μmol photons.m^{-2}.s^{-1} (Bonilla et al. 2012) to 19 μmol photons.m^{-2}.s^{-1} (Wojciechowski et al. 2016) and 16 to 26 μmol photons.m^{-2}.s^{-1} (Briand et al., 2004).

A number of authors have recognized the ability of *C. raciborskii* to grow at low light intensities, however several studies suggest that the difference between strains is very significant. Bouvy et al. (1999) in field studies noted the dominance of *C. raciborskii* in reservoirs with irradiance ranging from 63 to 140 μmol photons.m^{-2}.s^{-1}. In laboratory experiments, Wojciechowski et al. (2016) observed maximum growth above 50 μmol photons.m^{-2}.s^{-1}; Briand et al. (2004) in 80 μmol photons.m^{-2}.s^{-1}; Carneiro et al. (2009) above 100 μmol photons.m^{-2}.s^{-1}; Brasil et al. (2017) and Bolius et al. (2017) in 130 μmol photons.m^{-2}.s^{-1}; and Bonilla et al. (2012) in 135 μmol photons.m^{-2}.s^{-1}. Burford et al. (2016) claimed that the optimal intensity for growth varies between 50 and 150 μmol photons.m^{-2}.s^{-1}.

Burford et al. (2016) also claimed that Australian strains suffer photoinhibition at intensities above 100 μmol photons.m^{-2}.s^{-1} in laboratory experiments and between 200 and 400 μmol photons.m^{-2}.s^{-1} under field conditions. However, both Burford et al. (op cit.) as other researchers (Bonilla et al., 2012; Marinho et al., 2013; Willis et al., 2015, 2016; Wojciechowski et al., 2016; Xiao et al., 2017) emphasized the great intraspecific variation in light requirements and other environmental factors. Kokociński et al. (2017) analyzing *C. raciborskii* invasion and dominance in European aquatic environments, found no correlation with light availability and justifies it because of the great variability among strains in light requirements.

Pierangelini et al. (2014a), testing two strains isolated from Australia with different morphology (coiled and streng) and toxin production capacity at different light exposures, found 2.6 times higher I$_k$ for coiled and toxic strains. Bittencourt-Oliveira et al. (2011, 2012) have asserted that species morphology is directly related to light intensity, with a predominance of straight trichomes at intensities higher than 30 μmol photons.m^{-2}.s^{-1}, indicating that the spiraled morphotype is more susceptible to higher light intensities.

Despite the availability of light does not seem to be fundamental to the dominance of *C. raciborskii*, adaptation to this factor can change its ability to compete with other species of cyanobacteria (Bonilla et al., 2012; Marinho et al., 2013; Xiao et al., 2017). Moore et al. (2003) claim that the formation of akinetes occurs in organisms growing only at light intensity higher than 25 μmol photons.m^{-2}.s^{-1} and Wojciechowski et al. (2016) observed a significant variation in the size of trichomes in strains submitted to different light intensities.

3.3. Water column stability

According to Padisák (1997), Tucci & Sant'Anna (2003), Bonilla et al. (2016) and Dalu & Wasserman (2018), stratification can be a key factor for the dominance of *C. raciborskii*, given that higher cell densities correlate with periods of water column stratification. Although these authors have identified an increasing in density under

stratification conditions, they also suggest that growth can happen under mixing conditions. There remain contradictions in the evidence regarding the role of stratification in the dominance of this species. For example, in Brazil, *C. raciborskii* also dominates in shallow and mixed systems (Bouvy et al., 1999; Moura et al., 2015).

Padisák (1997) recorded *C. raciborskii* occurring at various depths within the epilimnion. Authors like Antunes et al. (2015) stated that stratified waters are favorable for this cyanobacterium, as it predominates under such conditions with low concentrations of dissolved nutrients. Based on the monitoring of a reservoir in Pernambuco, Brazil, Bittencourt-Oliveira et al. (2011) also concluded that stable stratification conditions during dry periods favor the growth of this species. However, Garcia (2007) and Bittencourt-Oliveira et al. (2011) did not observe significant reduction in the abundance of *C. raciborskii* in the phytoplankton community during the period of circulation.

Antunes et al. (2015) and Casali et al. (2017) noted a variation across the water depth gradient, as *C. raciborskii* are dominant at the surface but not in the bottom water. On the other hand, the substantial floating capability allows daytime migration between hypolimnium and epilimnion and prevents accumulation on the surface shading the deeper layers (Padisák, 1997). Corroborating this, Bittencourt-Oliveira et al. (2011) showed a negative correlation with depth. The greater water density at lower layers of the water column favors the coiled trichome form and is most suitable for its development.

In most publications we found that stratified environments favor the prevalence of *C. raciborskii*, but as this species may also predominate in non-stratified or polymictic environments (Barros et al., 2006; Von Sperling et al., 2008; Casali et al., 2017), this condition may not be as important as it is to other cyanobacteria such as *Microcystis* sp. (Calijuri et al., 2002).

3.4. pH and CO_2

Another important factor considered responsible for the dominance of *C. raciborskii* is the tolerance to high pH. This may be due to a direct effect of pH, since the percentage of CO_2 decreases as the pH rises, which may limit CO_2 availability for phytoplankton. Cyanobacteria, including *Cylindrospermopsis raciborskii*, have the ability to use other carbon sources when present, such as HCO_3. They are therefore good competitors in low

CO_2 and high pH conditions. (Holland et al., 2012; Burford et al., 2016).

According Padisák (1997), *C. raciborskii* is found between pH 6 to 10. Bouvy et al. (1999) observed a dominance of this species in waters with a pH range of 8.1 to 9.4. Others pH values were found by Saker et al. (2003), Hamilton et al. (2005), Gemelgo et al. (2008), Marinho et al. (2013), Recknagel et al. (2014) and Antunes et al. (2015), all between 6.9 and 10.

On the other hand, different pH ranges have been observed in Brazilian aquatic systems with dominance of *C. raciborskii* by Tucci & Sant'Anna (2003), Antunes et al. (2015) and Casali et al. (2017); these were 5.8 to 7.6, 5.5 to 9.9, and 3.9 to 7.1, respectively, showing the ability of the species to survive in both slightly acidic and extremely alkaline waters.

Using laboratory cultures, Holland et al. (2012) observed species death under pH 4.2, and an increased growth rate at higher pH values and HCO_3 concentrations. Wiedner et al. (2007), Yamamoto & Shiah (2012) and Karadžić et al. (2013) argued that the increasing in pH reflects intense photosynthetic cyanobacterial activity, due to proliferations, that remove H^+ ions from the water. Therefore, these organisms will be adapted to environments with higher pH.

Pierangelini et al. (2014a) stated that *C. raciborskii* presents major reorganization of its photosynthetic apparatus, in both function and structure, in response to increased CO_2 concentrations. According to Antunes et al. (2015), since the species can also grow in high concentrations of CO_2, increased CO_2 levels will probably not have a significant effect on its environmental performance. Therefore, *Cylindrospermopsis raciborskii* can optimize resources, such as carbon, when there are changes in their availability.

3.5. Salinity

The species has a preference for low-salinity conditions, with optimal growth in oligohaline water conditions (0.5-5 ppm) (Chapman & Schelske, 1997; Padisák, 1997; Karadžić et al., 2013; Antunes et al., 2015; Duval et al., 2018). Higher values of salinity (≥ 30 ppm) are considered limiting to its growth (Moisander et al., 2012); however, *C. raciborskii* has the capacity to dominate in brackish waters, particularly when there are enriched nutrient conditions (Calandrino & Paerl, 2011; Engström-Öst et al., 2015), or high concentrations of dissolved minerals, especially high sulfate concentrations (Briand et al., 2002). According to Antunes et al. (2015), climate

conditions that cause changes in precipitation can alter the salinity of estuarine systems and contribute to the dominance of the species in those ecosystems.

However, Chapman & Schelske (1997), Padisák (1997) and Moisander et al. (2012) reported the salinity tolerance threshold for the growth of the species as being between 0.5 and 5 ppm. Calandrino & Paerl (2011) reported that the species can withstand mesohaline conditions, with values between 7 and 8 ppm, only reducing its growth at concentrations higher than 8 ppm. Furthermore, Engström-Öst et al. (2015) indicated

C. raciborskii tolerance in salinity conditions ranging from 4.5 to 8 ppm.

3.6. Nutrients

The growth of *C. raciborskii*, in particular its ability to form blooms, is reported to be influenced by the concentrations of some nutrients that are typically observed in eutrophic environments (Yang et al., 2017). The biomass changes of most species of cyanobacteria are related to nutrient content in aquatic ecosystems and are summarized in Table 1.

Table 1. Some abiotic environmental factors that influence *C. raciborskii* dominance.

Variables	Details	References
Temperature	From 11 °C to 35 °C with optimal temperature near 23 °C.	Antunes et al. (2015), Berger et al. (2006), Bittencourt-Oliveira et al. (2011), Bonilla et al. (2012, 2016), Bouvy et al. (1999, 2000), Briand et al. (2002), Casali (2014), Chonudomkul et al. (2004), Dokulil (2016), Dufour et al. (2006), Engstrom-Ost et al. (2015), Everson et al. (2011), Fabre et al. (2010), Figueredo et al. (2014), Fuentes et al. (2010), Garcia (2007), Gemelgo et al. (2008), Hamilton et al. (2005), Jones & Sauter (2005), Kehoe et al. (2015), Kokociński et al. (2017), Maia-Barbosa et al. (2010), Mehnert et al. (2010), Padisák (1997), Recknagel et al. (2014, 2019), Saker et al. (2003), Soares et al. (2013), Souza et al. (1998), Thomas & Litchman (2016), Tucci & Sant'Anna (2003), Xiao et al. (2017).
Light	Optimal growth between 50 to 150 µmol photons.m^{-2}.s^{-1} with I$_k$ from 8 to 26 µmol photons.m^{-2}.s^{-1} with great interspecific variation.	Beamud et al. (2016), Bittencourt-Oliveira et al. (2011, 2012), Bolius et al. (2017), Bonilla et al. (2012), Bouvy et al. (1999), Brasil et al. (2017), Briand et al. (2004), Burford & Davis (2011), Burford et al. (2016), Carneiro et al. (2009), Engstrom-Ost et al. (2015), Kokociński et al. (2017), Marinho et al. (2013), Moore et al. (2003), Noyma et al. (2015), Padisák (1997), Pierangelini et al. (2014a), Willis et al. (2015, 2016), Wojciechowski et al. (2016), Xiao et al. (2017), Yamamoto & Shiah (2012).
Water column stability	Stable environments are favorable but not essential.	Antunes et al. (2015), Barros et al. (2006), Bittencourt-Oliveira et al. (2011), Bonilla et al. (2016), Bouvy et al. (1999), Casali et al. (2017), Dalu & Wasserman (2018), Garcia (2007), Moura et al. (2015), Padisák (1997), Tucci & Sant'Anna (2003), Von Sperling et al. (2008).
pH and CO$_2$	From 5.8 to 9.9 with optimal pH near 7.8. Ability to optimize carbon when there are changes in its availability.	Antunes et al. (2015), Bouvy et al. (1999), Burford et al. (2016), Casali et al. (2017), Gemelgo et al. (2008), Hamilton et al. (2005), Holland et al. (2012), Karadžić et al. (2013), Marinho et al. (2013), Padisák (1997), Pierangelini et al. (2014a), Recknagel et al. (2014), Saker et al. (2003), Tucci & Sant'Anna (2003), Wiedner et al. (2007), Yamamoto & Shiah (2012),
Salinity	From 0.5 ppm to 8 ppm with optimal growth in oligohaline conditions.	Antunes et al. (2015), Briand et al. (2002), Calandrino & Paerl (2011), Chapman & Schelske (1997), Duval et al. (2018), Engstrom-Ost et al. (2015), Karadžić et al. (2013), Moisander et al. (2012), Padisák (1997),
Nitrogen	Dominance in different concentrations of different nitrogen sources but with preference for ammonium.	Ammar et al. (2014), Antunes et al. (2015), Barros et al. (2015), Briand et al. (2002), Burford et al. (2006), Calandrino & Paerl (2011), Casali (2014), Engstrom-Ost et al. (2015), Everson et al. (2011), Karadžić et al. (2013), Lima (2015), Moustaka-Gouni et al. (2007), Padisák (1997), Tucci & Sant'Anna (2003), Vargas & Calijuri (2013), Wiedner et al. (2007)
Phosphorous	Ability to store phosphorus in the cell and grow in environments with low concentrations despite being associated with eutrophic environments.	Antunes et al. (2015), Bai et al. (2014), Barros et al. (2015), Bouvy et al. (2000), Briand et al. (2002), Burford & Davis (2011), Burford et al. (2016), Casali (2014), Fuentes et al. (2010), Isvánovics et al. (2000), Jones & Sauter (2005), Marinho et al. (2013), Padisák (1997), Tonetta et al. (2015), Wojciechowski (2013), Wu et al. (2012).
N:P ratio	Dominates in environments with a wide range of N:P ratios.	Burford et al. (2016), Casali (2014), Chislock et al. (2014), Kenesi et al. (2009), Kim et al. (2007), Vargas & Calijuri (2013).

3.6.1. Nitrogen concentrations

Tolerance to low environmental nitrogen concentrations is related to the presence of specialized cells called heterocytes. These cells have a thick cell wall providing an anaerobic intracellular environment. This is required for fixation of atmospheric nitrogen (N_2) and allows C. *raciborskii* to survive in environments with dissolved nitrogen deficiency (Padisák, 1997; Moustaka-Gouni et al., 2007; Wiedner et al., 2007; Everson et al., 2011; Antunes et al., 2015; Barros et al., 2015; Burford et al., 2016).

In addition, this species has a high affinity for the ammonium ion that represents a more available nitrogen source (Antunes et al., 2015; Barros et al., 2015; Padisák, 1997). Nevertheless, it is possible to find *C. raciborskii* in environments with low concentrations of ammonia (Casali et al., 2017; Engström-Öst et al., 2015). Experiments by Barros et al. (2015) and Lima (2015) in Brazilian reservoirs, showed that *C. raciborskii* prefers and grows faster using ammonium ions, followed by nitrate and urea.

Ammar et al. (2014) argued that in the absence of nitrate the species declines rapidly and at higher nitrate concentrations the species continues to have a low biomass. As such, *C. raciborskii* loses its rapid growth advantage when nitrate forms the sole source of nitrogen. Moreover, Antunes et al. (2015) found *C. raciborskii* heterocytes to be fewer or absent in high concentrations of NO_3, thereby indicating the consumption of NO_3 as a source of nitrogen. However, Briand et al. (2002) explained the low percentage of heterocytes in lower nitrate concentrations by the species' preference for ammonium ion as nitrogen source. Additionally, Casali (2014) noted the presence of heterocytes in most trichomes, even without nitrogen limitation, in a sub-tropical reservoir.

Padisák (1997) argued that nitrogen fixation is a factor that contributes to the dominance of *C. raciborskii*. However, Tucci & Sant'Anna (2003), Burford et al. (2006), Moustaka-Gouni et al. (2007) and Karadžić et al. (2013) dismissed the importance of this strategy for the intensive development of the species. They argued that, at a number of study sites, only a small number of trichomes with heterocytes have been observed. At these sites, nitrogen was never a limiting factor, primarily due to the presence of ammonium ion. In these same studies, the species was found in large quantities when NH_4^+ and NO_3 were present in high concentration.

Ammar et al. (2014) showed that *C. raciborskii* has the capacity to grow in NH_4^+ free conditions and at low concentrations of ammonium ion; however, low growth rates were demonstrated under conditions of NH_4 shortage, whereas under high concentrations there was a constant increase in biovolume. This finding was corroborated by Briand et al. (2002), Calandrino and Paerl (2011), Antunes et al. (2015) and Lima (2015). These authors suggest that cyanobacteria have a greater affinity for ammonium ion as the sole source of nitrogen, giving them a competitive advantage.

3.6.2. Phosphorus concentrations

Tolerance to low phosphorus concentration is due to a higher absorption capacity and affinity compared to other photoautotrophic organisms. This suggests that *C. raciborskii* is opportunistic with respect to dissolved inorganic phosphorus (Isvánovics et al., 2000). Both inorganic phosphorus and total phosphorus concentrations vary widely in aquatic environments dominated by *C. raciborskii* (Burford & Davis, 2011; Wu et al., 2012; Wojciechowski, 2013; Burford et al., 2016), and this ability can be important for the formation of akinetes (Antunes et al., 2015; Tonetta et al., 2015).

Padisák (1997), Bai et al. (2014) and Antunes et al. (2015) have observed that *C. raciborskii*, under conditions of limited environmental phosphate, displays high affinity absorption and an ability to store different sources of organic phosphorus in the cytoplasm in the form of polyphosphates to support their growth. In addition, Willis et al. (2017, 2019) evaluated the ability of different strains of *C. raciborskii* to obtain and reserve phosphorus. They showed that this ability may differ between strains, implying that growth may occur under conditions of widely varying phosphorus availability.

Briand et al. (2002), Fuentes et al. (2010), Wu et al. (2012), Marinho et al. (2013), Bai et al. (2014), Antunes et al. (2015), Barros et al. (2015) and Casali et al. (2017) considered *C. raciborskii* to be opportunistic regarding dissolved inorganic phosphorus (DIP) use. They cite its apparent ability to regulate its physiologic metabolism and to adapt to low environmental DIP concentrations with increased alkaline phosphatase production. This adjustment mechanism reduces phosphorus limitation to the cell.

Jones & Sauter (2005) observed that the presence of *C. raciborskii* was closely related to high concentrations of total phosphorus (TP). However,

Bouvy et al. (2000) found that the abundance of the species was not directly dependent on TP concentrations. The Brazilian reservoirs they studied present phosphorus deficiency but dominance of the species.

3.6.3. N:P ratio

Kim et al. (2007) reported that the N:P ratio is a determinant of cyanobacteria proliferation. In bioassays conducted on the addition of phosphorus and nitrogen to phytoplankton, they found that the increasing from 4:1 to 30:1 N:P ratio did not result in increasing in the growth of *C. raciborskii*. On the other hand, Burford et al. (2016) showed higher concentrations of *C. raciborskii* cells in high N:P ratios.

Vargas & Calijuri (2013) observed that in laboratory experiments with strains of *C. raciborskii* isolated from the Itupararanga reservoir, a high N:P ratio (28:1) was not associated with reduced growth when interacting with *M. contortum*. Chislock et al. (2014) found *C. raciborskii* comprising 100% of the total biomass of phytoplankton in a lake in the US under low (7:1) and high (122:1) N:P ratios.

Kenesi et al. (2009) proposed that *C. raciborskii* has the capacity to grow faster and maintain high biomass in phosphorus-limited conditions if NH_4 or NO_3 are available. Recknagel et al. (2019) have also demonstrated rapid growth in tropical nitrogen-limited environments. Cunha & Calijuri (2011) and Casali et al. (2017) observed the species in the Itupararanga reservoir under phosphorus limitation, but nitrate availability.

4. Biotic Factors

4.1. Allelopathy

The ability to produce and secrete allelopathic substance1s has recently been suggested to have contributed to the geographic expansion of *C. raciborskii*. This was first demonstrated in a study of a lake in southeastern Brazil, where this species had become dominant (Figueredo et al., 2007). Exudates from different strains resulted in strong inhibitory effects on the photosynthetic activity of other algae (Antunes et al., 2012). Allelopathy was considered by the authors to be a useful competitive mechanism, and a potentially significant factor in *C. raciborskii*'s propagation in bodies of water in temperate climates (Figueredo et al., 2007; Figueredo & Giani, 2009; Leão et al., 2009).

The success of allelopathic activity in invasive species can be explained by the fact that native species have not had long periods of coexistence with them, and therefore have not evolved to tolerate the allelochemicals produced (Fistarol et al., 2004). Leão et al. (2009) tested the allelopathic effects of several strains of *C. raciborskii* in Portuguese reservoirs. The LEGE 99043 strain was shown to significantly inhibit the growth of the microalgae *Ankistrodemsus falcatus*. A later study by Antunes et al. (2012) showed that the activity of the allelopathic LEGE 99043 strain was influenced by different environmental parameters. Phosphorus deprivation, high temperature and light intensity resulted in greater allelopathic activity, suggesting that ecophysiological allelopathy may have a high degree of relevance. In particular, the increasing in allelopathic activity at high temperatures may be important considering the role of climate warming in the spread of the species in temperate climates.

Dantas et al. (2008) and Soares et al. (2009) analyzed samples from a tropical reservoir, where populations of this species and *Microcystis aeruginosa* coexisted naturally. Inhibition of *M. aeruginosa* growth was observed after exposure to exudates from mixed cultures with a high proportion of *C. raciborskii* (Mello et al., 2012). This result demonstrates that allelopathy may also be important in explaining the seasonal dynamics of the species. On the other hand, *C. raciborskii* showed the ability to overcome *Microcystis* sp. in a mixed culture by producing compounds, not yet characterized as allelopathic, that mimic the action cylindrospermopsin (Burford et al., 2016; Rzymski et al., 2014).

Laboratory experiments performed by Vargas & Calijuri (2013) regarding the interaction between *C. raciborskii* and the Chlorophyceae *Monoraphidium contortum,* in which environments with varying degrees of nutrient concentration were simulated, demonstrated that *C. raciborskii* growth was not inhibited by the presence of *M. contortum*. Furthermore, as showed by Casali et al. (2017) in a mesotrophic subtropical reservoir, these cyanobacteria were capable of coexisting with *M. contortum*. According to the authors, despite the coexistence, the *C. raciborskii* biomass was on average 500 times greater than that of *M. contortum*.

4.2. Herbivory

The consumption by zooplankton can limit the growth of cyanobacteria. However, cyanobacteria display a number of mechanisms that reduce

this predation, including size and shape of the cell, nutritional quality and toxicity. Because of low levels of polyunsaturated fatty acids compared to other phytoplanktic groups – an important nutrient for zooplankton development – the consumption of these cyanobacteria can be disadvantageous, reducing the growth, reproduction and, consequently, the survival of its predator (Tucci & Sant'Anna, 2003; Leonard & Paerl, 2005; Magalhães, 2014; Burford et al., 2016).

The earliest study about herbivory of *C. raciborskii* was conducted by Seenayya (1971), who noted zooplankton peaks preceded by phytoplankton growth in a shallow pond in India. A setback in the development of zooplankton was identified particularly in the presence of *C. raciborskii*. The same was observed by Branco & Senna (1994), a zooplanktic species from the Paranoá reservoir in Brazil was shown to be generally incapable of consuming this permanently occurring *C. raciborskii* at high densities.

Studies by Berger et al. (2006) in a lake in Senegal, Africa, showed that the proliferation of *C. raciborskii* consists of toxic and non-toxic clones and the authors concluded that the low presence of toxic strains in environmental samples was due to low herbivory pressure. Wiedner et al. (2007) concluded that herbivores do not play an important role in population control of *C. raciborskii*, but noted that large species such as *Daphnia magna* or *D. pulex,* which are capable of ingesting *C. raciborskii,* were not present in the lakes they studied. However, Weithoff et al. (2017) have demonstrated, in experiments on mesocosms, that top-down control can occur under specific conditions.

In experiments conducted by Fabre et al. (2017), where highly toxic strains of *C. raciborskii* were ingested by *Neothyris iheringi*, toxicity was shown to play a more important role than morphology in determining clearance rates of this zooplankton. In addition, subtropical species of zooplankton, such as Cladocera and Copepoda, demonstrate a weak

potential for predatory control of *C. raciborskii,* thus favoring the growth and dispersion of this cyanobacterium in aquatic ecosystems. Biotic factors related to dominance of *C. raciborskii* are summarized in Table 2

5. Ecotypes or Metabolic Plasticity?

An analysis of *C. raciborskii*'s environmental requirements demonstrates its great ability to survive in different conditions. The ecological success of *Cylindrospermopsis* can be attributed to ability to tolerate a range of enviromental conditions. Ecophysiologic plasticity, or the existence of ecotypes with different preferences and environmental tolerances (Berger et al., 2006; Bonilla et al., 2012), has been noted by several authors (Chonudomkul et al., 2004; Fuentes et al., 2010; Bonilla et al., 2012; Gomes et al., 2013; Soares et al., 2013; Pierangelini et al., 2014b; Antunes et al., 2015; Wojciechowski et al., 2016; Casali et al., 2017; Fabre et al., 2017; Xiao et al., 2017).

Metabolic plasticity is the process by which a single genotype is capable of producing different phenotypes (organisms with different morphological and physiological characteristics) under changing environmental conditions (Pigliucci, 2001). This may be the result of change in expressed gene activity or rearrangement of information contained within a genotype (Morales et al., 2002; Comte et al., 2013).

Although plasticity should lead to the expression of a more appropriate phenotype in a given environment, there are costs to this strategy (Morales et al., 2002). According to Pigliucci (2001), the costs relate to five concepts: the maintenance of the genetic infrastructure capable of responding to the need for plasticity; the production of a phenotype by way of plasticity mechanisms; the acquisition of information from the environment; the developmental instability that results from the ability to modulate the phenotype; and the

Table 2. Some biotic factors that influence *C. raciborskii* dominance.

Factor	Details	References
Allelopathy	Strong inhibitory effects on the photosynthetic activity of different algae.	Antunes et al. (2012), Antunes et al. (2015), Burford et al. (2016), Casali (2014), Dantas et al. (2008), Engstrom-Ost et al. (2015), Figueredo et al. (2007), Fistarol et al. (2004), Leão et al. (2009), Mello et al. (2012), Rzymski et al. (2014), Soares et al. (2009), Vargas & Calijuri (2013).
Herbivory	Generates a setback in the development of zooplankton, but the opposite does not appear to be an important factor.	Berger et al. (2006), Branco & Senna (1994), Burford et al. (2016), Fabre et al. (2017), Leonard & Paerl (2005), Magalhães (2014), Padisák et al. (1984), Seenayya (1971), Tucci & Sant'Anna (2003), Wiedner et al. (2007),

interference with the binding and interaction of plasticity genes.

By contrast, ecotypes are defined as groups that are genetically and phenotypically distinct from a major population and adapted to local climatic conditions (Hufford & Mazer, 2003). They have the potential to become a single species, provided that there is some sort of barrier preventing the exchange of genes (Morales et al., 2002; DeLong & Karl, 2005; Wiedner et al., 2007; Willis et al., 2015, 2016). Thus, ecotypes describe a discrete set of defined strains according to the sequence of core genes. This provides a stable basis for taxonomy (Kumar et al., 2015). Metabolic plasticity refers to a species that has several genes for a specific factor (Comte et al., 2013), and ecotype refers to a species that may (or may not) have active genes for a specific factor (Kumar et al., 2015).

The bacterial genome is characterized by diversity and can be extremely dynamic. It may acquire and lose genes, forming a genomic assembly adapted to each specific habitat (Kashtan et al., 2014; Kümmerli et al., 2009; Lima-Bittencourt et al., 2007). Changes responsible for the plasticity of the genome mostly result from horizontal gene transfer. Point mutations in enzymes that represent the metabolic bottlenecks increase the diversity of substrates or change the enzymes' specificities. However, increased diversity can also occur via vertical transfer, where enzymes are incorporated that transform novel compounds already used in another metabolism (Tooming-Klunderud et al., 2013).

Corno & Jürgens (2006) suggested that general mechanisms of direct grazing and size selection, as well as chemical induction of morphotypes, can determine the size structure of the population of a bacterial strain with high phenotypic plasticity. Huber et al. (2017), analyzing populations of picocyanobacteria, described great phenotypic plasticity (formation of aggregations) influenced by environmental factors and predation.

In bacteria, there are also some examples of the existence of different ecotypes. Sher et al. (2011) studied the *Prochlorococcus marinus* and observed that this species is divided into at least two ecotypes, with different capacities for using light, nitrogen and phosphorus. Koops et al. (1991) studied 96 *Nitrosomonas* sp. strains – a type of ammonia-oxidizing bacteria – and suggested the existence of at least seven ecotypes. Moreover, Fabre et al. (2017) showed differences in the morphological and toxicological profiles of two different strains of *C. raciborskii* producing paralytic shellfish poison. This supports the hypothesis that these species have multiple ecotypes. Hoffmann et al. (2017) studied a set of genes from two strains of *C. raciborskii* isolated in Brazil. The genetic differences identified pointed to two different ecotypes.

It is not yet entirely possible to determine whether the distribution of *C. raciborskii* in different climates is the result of high metabolic plasticity, allowing it to explore various environments differently, or the existence of different ecotypes that will predominate in specific conditions. To clarify this issue, we suggest further studies on environmental needs with isolated strains, differentiated by molecular biology, from several different ecosystems. One option would be to compare the genetic material of species from different environments. If metabolic plasticity was the underlying factor, DNA differences would be small (Corno and Jürgens, 2006), but if they are different or show a greater degree of difference between the environments the hypothesis of ecotype would better explain the predominance of this species (Kumar et al., 2015). The problem is that a large amount of data is needed to make this comparison, including large studies of gene markers.

Another approach would be to test strains isolated from a given environment under conditions found in a different environment. This could demonstrate whether strains can adapt to different conditions by metabolic plasticity or survive and grow only under the conditions in which they were selected (ecotypes). Due to large differences, mainly related to the limits of growth and development found in some studies (Chapman and Schelske, 1997; Padisák, 1997; Tucci & Sant'Anna, 2003; O'Brien et al., 2009; Calandrino & Paerl, 2011; Bittencourt-Oliveira et al., 2012; Moisander et al., 2012; Engström-Öst et al., 2015), the possibility of different ecotypes seems the most appropriate hypothesis, with important implications for the modeling and use of organisms as bioindicators (Xiao et al., 2017). Wiedner et al. (2007), Wu et al. (2011), Zhang et al. (2014) and Willis et al. (2015, 2016, 2018) found major genetic differences between *C. raciborskii* strains from different bodies of fresh water, thereby suggesting the presence of ecotypes.

6. Conclusions

From a detailed analysis of the recent literature on the key factors responsible for the dominance and widespread distribution of *C. raciborskii*

in natural environments throughout the world supplemented by knowledge from laboratory experiments, we conclude that:

- The optimal temperature is about 23 °C, but may be dominant in environments with temperatures between 11 to 35 °C;

- The optimal light intensity is between 50 and 150 µmol photons.m^{-2}.s^{-1}. Low I_k indicates a good ability to survive and grow in aquatic environments with very low light intensities;

- *C. raciborskii* prefers stable environments, but this is not essential;

- The ability to optimize carbon use when there are changes in its availability, and to survive in alkaline environments, is important;

- *C. raciborskii* prefers oligohaline conditions and interferes in the photosynthetic activity of different algae by producing allelopathic substances;

- Herbivory does not play an important role in the control of the *C. raciborskii* population, but it may be important in the selection of ecotypes;

- Nutrients have a different influence: different concentrations of different sources of nitrogen are supported, with a preference for ammonia. In relation to phosphorus, the species can grow in conditions of high or low concentrations due to its capacity to reserve phosphorus in the cell. However, *C. raciborskii* is always associated with eutrophic environments.

It is clear that a better understanding of this cyanobacterium will have implications for the methods of species control, as well as complementing the knowledge about their function in aquatic ecosystems. It is not entirely possible to determine if the distribution of *Cylindrospermopsis raciborskii* in different climates is a result of high metabolic plasticity, allowing it to explore various environments in different ways, or of the existence of distinct ecotypes that predominate under specific conditions. However, due to the large variations in the limits of growth and development found in some studies, the possibility of distinct ecotypes seems to be the most appropriate hypothesis.

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