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Appearance of *Cylindrospermopsis raciborskii* in winter in an artificial pond in northern Taiwan

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Abstract – The seasonal dynamics of *Cylindrospermopsis raciborskii* was investigated from June 2011 to December 2013 in a small artificial pond in northern Taiwan. The abundance of *C. raciborskii* increased from late February to early April 2012 when the water temperature ranged from 16.4 to 21.7 °C and from mid-August 2012 to mid-February 2013 as the water temperature decreased from about 27 °C to below 20 °C; it peaked in mid-February 2013 when the water temperature was 16.3 °C. In the summer months, the abundance of *C. raciborskii* was very low and sometimes undetectable. A laboratory experiment using a strain that was isolated from the pond suggested that the dominance of *C. raciborskii* in low-temperature seasons could be attributed to its tolerance of, not preference for, low temperatures. Contrary to the results of this study, our earlier survey conducted in the same pond from August 2009 to January 2011 showed that the abundance of *C. raciborskii* was low in winter and increased in summer. Environmental changes in the study pond and/or the appearance of a different ecotype was assumed to be responsible for the change in the dynamics of *C. raciborskii*.

Key words: *Cylindrospermopsis raciborskii* / growth / seasonal succession / temperature

Introduction

Cylindrospermopsis raciborskii (Woloszynska) Seenayya & Subba Raju is a filamentous cyanobacterium that is found in tropical, subtropical and temperate regions. The worldwide distribution of *C. raciborskii* is thought to be a consequence of its expansion from tropical regions to temperate parts of the globe (Padisák, 1997). Environmental change on a global scale is assumed to have enabled it to survive at higher latitudes (Padisák, 1997; Briand *et al.*, 2004; Wood *et al.*, 2014). Additionally, its ability to produce resting spores, called akinetes (Padisák, 1997; Chonudomkul *et al.*, 2004; Haande *et al.*, 2008), and the presence of low-temperature adaptive strains (Chonudomkul *et al.*, 2004; Piccini *et al.*, 2011), appear to have also played an important role in the expansion of *C. raciborskii*.

Although *C. raciborskii* can maintain large populations perennially in tropical regions, it normally becomes dominant only in high-temperature seasons at higher latitudes (Saker and Griffiths, 2001; Hamilton *et al.*, 2005; Moustaka-Gouni *et al.*, 2007; Yamamoto and Shiah, 2012). Laboratory studies have shown that the growth of *C. raciborskii* generally increases with temperature up to approximately 30 °C (Saker and Griffiths, 2000; Briand *et al.*, 2004; Chonudomkul *et al.*, 2004). Chonudomkul *et al.* (2004) demonstrated that *C. raciborskii* strains that were isolated in Thailand were composed of low-temperature adaptive and non-adaptive strains, while all strains that were isolated from Japan were adaptive to low temperatures. They showed that all strains tested grew at temperatures as low as 15–17.5 °C and exhibited optimal growth at 25–35 °C (Chonudomkul *et al.*, 2004). Therefore, the growth of low-temperature adaptive strains is also assumed to increase in summer.

It is noteworthy that, in some cases, temperature seemingly influences the growth of *C. raciborskii* in an unexpected manner. Kokociński and Soininen (2012) investigated the distribution of *C. raciborskii* in Polish lakes, and showed that the cyanobacterial biomass was negatively correlated with summer temperatures. Some reports have described the dominance of *C. raciborskii* in low-temperature seasons (Dokulil and Mayer, 1996; Bonilla *et al.*, 2012). Most investigators recognize temperature as a primary factor in regulating the growth of *C. raciborskii* but agree that numerous environmental

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*Corresponding author: `yamamoto@euglena.jp` factors influence its dynamics in nature (Padisák, 1997). However, relatively little attention has been paid to the underlying reasons for such atypical phenomena.

In Taiwan, *C. raciborskii* is widely distributed in eutrophic ponds (Yamamoto *et al.*, 2011). Surveys of a pond in northern Taiwan have demonstrated that *C. raciborskii* exhibits typical seasonal dynamics, with a low population density in winter and dominating in summer (Yamamoto and Shiah, 2012; Yamamoto *et al.*, 2013). However, extended monitoring has shown that *C. raciborskii* sometimes exhibits atypical seasonal dynamics. This report describes the disappearance of *C. raciborskii* in summer and its appearance in winter in a small pond in northern Taiwan. The findings of this study may provide new insights into the ecophysiological aspects of *C. raciborskii* and thus improve our understanding of its dynamics in ecosystems.

Materials and methods

Study site and sampling

A field survey was performed from June 2011 to December 2013 in a shallow artificial pond (110 m^2 surface area, 0.3 m constant depth) in Taipei, northern Taiwan (25°02′21″N, 121°37′02″E). The water balance of the pond was governed by rainfall, evaporation, and the outflow of excess water through a drain (60 mm Ø) at 0.3 m above the bottom. The pond lies between a building and large trees, which protect it from direct sunlight.

Almost weekly monitoring of water temperature, pH, nitrate, nitrite, ammonium, total nitrogen (TN), total phosphorus (TP) and phytoplankton abundance was conducted according to the methods described in Yamamoto and Shiah (2012). In the present study, the concentration of total dissolved phosphorus (TDP), instead of soluble reactive phosphorus, was measured by applying the method for the measurement of TP to the GF/C filtrate. *C. raciborskii* was identified based on its morphological characteristics (Horecká and Komárek, 1979; Komárek and Kling, 1991). A least square linear regression of the natural logarithm of *C. raciborskii* abundance versus time was performed for each growing phase and the slopes of the regression lines were used to obtain net growth rates (d^{-1}).

Laboratory experiments

The impact of temperature on the growth of *C. raciborskii* was examined using a culture strain that was isolated from the pond in January 2013. A non-axenic stock culture was maintained in screw-capped test tubes (16 × 150 mm) containing 8 mL of modified C medium (Yamamoto and Shiah, 2014) under standard conditions of 25 °C and a 12 h:12 h light–dark cycle with a light intensity of 60 μmol photons $m^{-2}.s^{-1}$. After 14 days of incubation, the culture was inoculated into glass test tubes (20 × 150 mm) containing 13 mL of medium. Triplicate cultures were incubated for 15 days in a temperature-gradient incubator RI-105 (Firstek, Taipei, Taiwan) at four temperatures (15, 20, 25 and 30 °C) under the standard light condition. Aliquots of 0.5 mL were taken from each culture every three days to determine the cyanobacterial abundance according to the methods described in Yamamoto and Shiah (2014). Growth was evaluated using the formula $(\ln N_t - \ln N_{t-3})/3$, where t is the day of sampling ($t = 3$, 6, 9, 12 and 15) and N_t is the abundance on day t. The highest values at each temperature were adopted as specific growth rates (d^{-1}).

Data analysis

Correlation between two pairs of variables was assessed by Pearson's correlation coefficient test. Values of $P < 0.05$ were considered to be statistically significant.

Results

Physicochemical variables

The water temperature ranged between 13.9 and 29.9 °C (Fig. 1). The highest temperatures in 2011, 2012 and 2013 were 29.2, 29.9 and 29.3 °C, respectively, all of which were recorded in July. High pH values (8.25–10.45) were measured from June to November 2011 (Fig. 1). The pH decreased in December 2011 and then fluctuated between 6.76 and 8.93 until December 2013.

The concentrations of ammonium, nitrite and nitrate exhibited no significant long-term trend but reached peaks simultaneously (Fig. 2). The mean concentrations of nitrate, nitrite and ammonium were 1.59, 0.16 and 2.41 μmol.L^{-1}, respectively. The concentration of TN fluctuated between 48.3 and 434.3 μmol.L^{-1}. A weak but significant positive correlation was found between TN concentration and temperature ($n = 125$, $r = 0.20$, $P < 0.05$). The TDP concentrations averaged 0.51 μmol.L^{-1}, with relatively little variation throughout the study period. The concentrations of TP greatly exceeded those of TDP, ranging from 2.11 to 18.2 μmol.L^{-1}. A significant positive correlation was found between TP and TN concentrations ($n = 125$, $r = 0.84$, $P < 0.001$).

Phytoplankton dynamics

The phytoplankton assemblage was dominated by cyanobacteria, diatoms and green algae (Fig. 3). From June 2011 to April 2013, the contribution of diatoms to the total phytoplankton abundance rarely exceeded 10%, but diatoms became an important component of phytoplankton from July 2013, owing to the massive growth of *Aulacoseira granulata* (Ehrenberg) Simonsen. A cyanobacterial bloom in September 2011 was composed mainly of *Microcystis aeruginosa* Kützing (Kützing), which

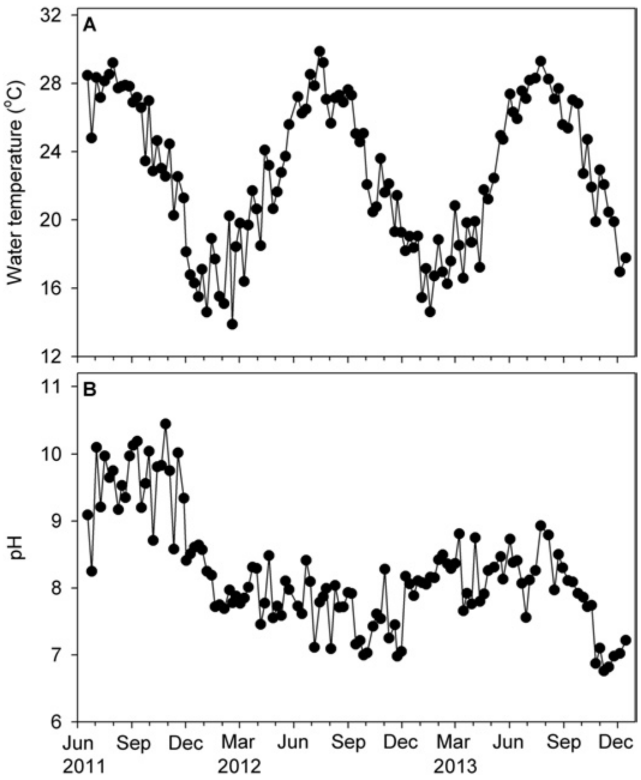

Fig. 1. Variations in water temperature (A) and pH (B) from June 2011 to December 2013 in the study pond in northern Taiwan.

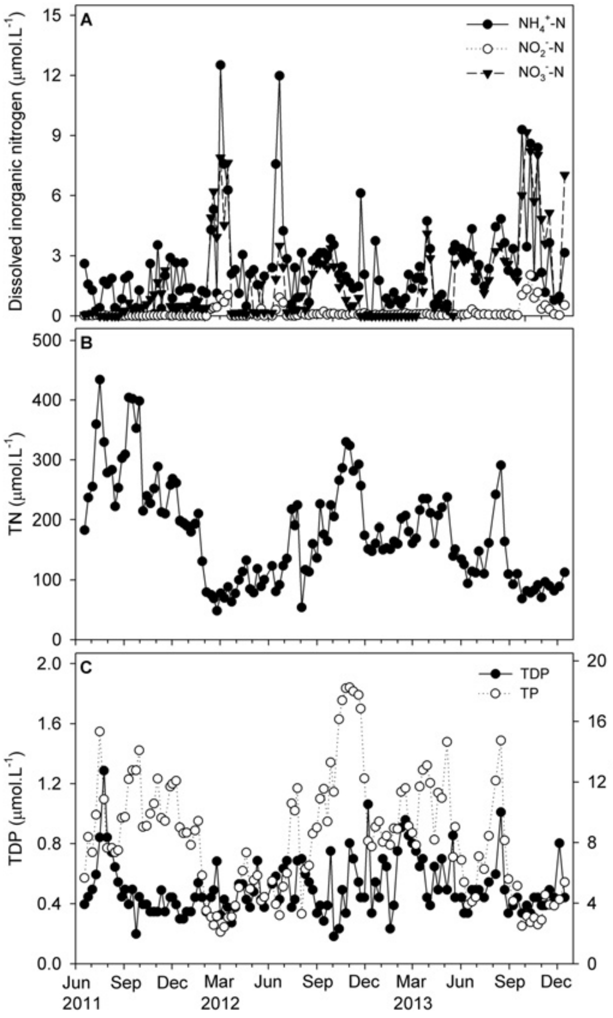

Fig. 2. Variations in concentrations of dissolved inorganic nitrogen (A), total nitrogen (B) and phosphorus (C) from June 2011 to December 2013 in the study pond in northern Taiwan.

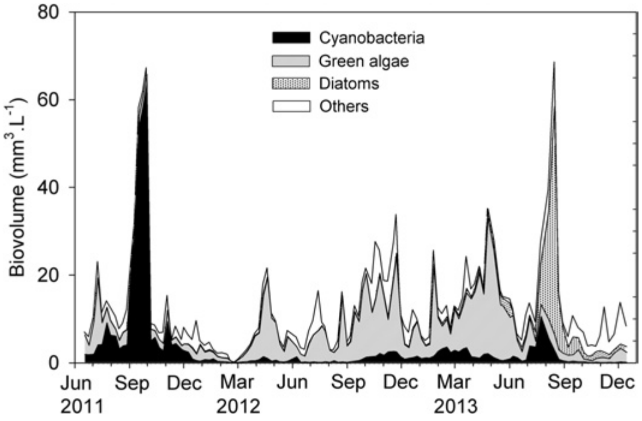

Fig. 3. Variation in abundance of phytoplankton from June 2011 to December 2013 in the study pond in northern Taiwan.

accounted for 80.1–93.5% of the total phytoplankton. *M. aeruginosa* was the main contributor to the cyanobacterial abundance, except in July 2011 and from late January to March 2013, when *C. raciborskii* became dominant. Green algae such as *Dimorphococcus lunatus* A. Braun, *Pediastrum duplex* Meyen and *Scenedesmus* spp. were dominant from December 2011.

Seasonal dynamics of *Cylindrospermopsis raciborskii*

The abundance of *C. raciborskii* increased from mid-June 2011 and reached 2.1 mm^3.L^{-1} in mid-July, before rapidly declining (Fig. 4). *C. raciborskii* was not observed from August 2011 to late February 2012. A small peak of *C. raciborskii* abundance appeared in mid-April 2012, but its abundance was low and sometimes immeasurable during the summer months. The abundance of *C. raciborskii* started to increase from September 2012, reaching 2.7 mm^3.L^{-1} in mid-February 2013, when it dominated the phytoplankton community. From late March 2013, the abundance of *C. raciborskii* rapidly declined and *C. raciborskii* disappeared from the water from May.

Throughout the monitoring, steady increases in the abundance of *C. raciborskii* were observed in four periods – from mid-June to mid-July 2011 (24.8–28.5 °C), from late February to early April 2012 (16.4–21.7 °C), from mid-August to mid-November 2012 (19.3–27.6 °C) and from mid-December 2012 to mid-February 2013 (14.6–19.1 °C). The net growth rates during these periods were 0.063 d^{-1} ($n = 5$, $r = 0.96$, $P < 0.05$), 0.087 d^{-1} ($n = 7$, $r = 0.94$, $P < 0.01$), 0.104 d^{-1} ($n = 13$, $r = 0.98$, $P < 0.001$) and 0.063 d^{-1} ($n = 10$, $r > 0.99$, $P < 0.001$), respectively.

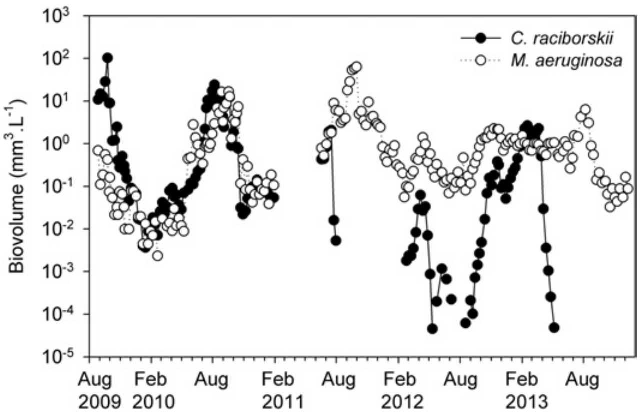

Fig. 4. Variations in abundance of *Cylindrospermopsis raciborskii* and *Microcystis aeruginosa* from August 2009 to December 2013 in the study pond in northern Taiwan. Data from August 2009 to January 2011 are sourced from Yamamoto and Shiah (2012). Sampling was not conducted from February to May 2011.

Overall, a significant inverse correlation existed between ln-transformed *C. raciborskii* abundance and temperature ($n = 60$, $r = -0.40$, $P < 0.01$).

Laboratory experiments

The growth of *C. raciborskii* increased with temperature; the final yields of *C. raciborskii* at 15, 20, 25 and 30 °C were 0.59, 2.11, 4.49 and 8.46 mm^3.L^{-1}, respectively (Fig. 5). The highest specific growth rate (0.50 d^{-1}) was obtained at 30 °C.

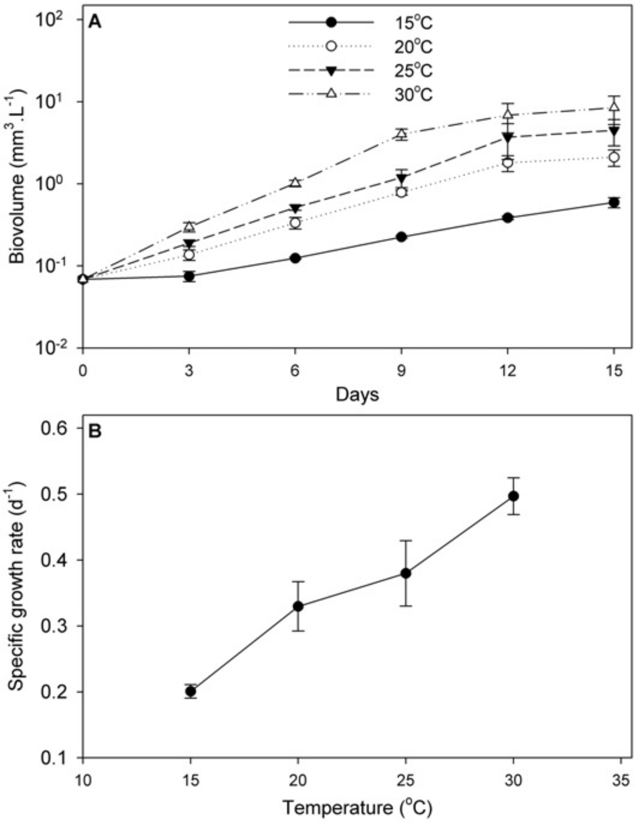

Fig. 5. Growth of *Cylindrospermopsis raciborskii* at five temperatures (A) and relationship between the specific growth rate and temperature (B). Error bars denote SD ($n = 3$).

Discussion

In the present study, *C. raciborskii* grew steadily and became dominant in winter in a small pond in northern Taiwan. This observation can be regarded as atypical, since *C. raciborskii* rarely becomes dominant in low-temperature seasons. A limited amount of information is available on the dominance of *C. raciborskii* in low-temperature seasons. In the case of Alte Donau in Austria, in which *C. raciborskii* dominated the cyanobacterial population, the abundance of *C. raciborskii* increased with temperature up to 15–18 °C but declined as the temperature increased further (Dokulil and Mayer, 1996). Bonilla *et al.* (2012) reported the formation of a bloom of *C. raciborskii* at 11 °C in a subtropical lake in Uruguay. However, a temperature of 11 °C appears to be below the threshold for the growth of *C. raciborskii* (Chonudomkul *et al.*, 2004), so the 'bloom' of *C. raciborskii* at such a low temperature might have been a remnant of a bloom that had occurred in the preceding summer.

One might assume that the *C. raciborskii* that appeared in the pond prefers low temperatures, but the laboratory experiment demonstrated that the *C. raciborskii* strain isolated from the pond, like other strains (Briand *et al.*, 2004; Chonudomkul *et al.*, 2004), preferred high temperatures for growth. The tested strain appeared to be adaptive to low temperatures since it showed moderate growth at 15 °C at which low-temperature non-adaptive strains show no or limited growth (Chonudomkul *et al.*, 2004). The water temperatures that were measured in winter were well below the optimal temperature for the growth of *C. raciborskii* but were mostly high enough to allow it to grow, leading to the conclusion that the large populations of *C. raciborskii* in the study pond in low-temperature seasons were reached through suboptimal growth. Although bloom-forming cyanobacteria generally prefer high temperatures and thereby become dominant in summer, tolerance for low temperatures can also be critical in enabling cyanobacteria to dominate in winter. For example, *Aphanizomenon flos-aquae* Ralfs ex Bornet et Flahault reportedly forms blooms in low-temperature seasons in Lake Biwa (Ichise *et al.*, 2000) and Lake Yogo (Tsujimura *et al.*, 2001) in Japan. Given the fact that *A. flos-aquae* can grow at temperatures as low as 8 °C and exhibits optimal growth at 23–29 °C (Tsujimura *et al.*, 2001), the dominance of *A. flos-aquae* in low-temperature seasons is accounted for by its tolerance for low temperatures.

The abundance of *C. raciborskii* in mid-July 2011 (2.1 mm^3.L^{-1}) was far lower than the peaks in late September 2009 (102.5 mm^3.L^{-1}) and early August 2010 (24.1 mm^3.L^{-1}) (Fig. 4), implying that the rapid decline in the abundance in late July 2011 occurred in the middle of the formation of a bloom. Rainfall is a factor that can rapidly – although often only temporarily – reduce the abundance of *C. raciborskii* during the growing season (Yamamoto *et al.*, 2013). However, no strong rainfall was recorded from mid- to late July 2011 in Taipei (Central Weather Bureau, 2013). A low summer temperature prevents the development of *C. raciborskii* blooms (Hamilton *et al.*, 2005), but the summer temperature in 2011 was as high as in previous years (Yamamoto and Shiah, 2012). The pH values in July 2011 were lower than those measured in previous summers (Yamamoto and Shiah, 2012). *C. raciborskii* requires a high pH for continuous growth (Padisák, 1997), but its photosynthetic activity elevates pH, complicating the relationship between pH and the growth of *C. raciborskii*. Nevertheless, pH is reasonably excluded from factors that limited *C. raciborskii* growth in July 2011 given its high values during this period. Additionally, no notable change in nutrient concentrations was observed in late July. Consequently, biotic factors may have played a central role in controlling the growth of *C. raciborskii* in this period.

The abundance of *M. aeruginosa* increased in late July 2011 when the abundance of *C. raciborskii* was rapidly decreasing, suggesting that the environmental conditions during this period favored the growth of *M. aeruginosa*. Notably, the dominant cyanobacterial species in the study pond has been shifting from *C. raciborskii* to *M. aeruginosa* in recent years (Fig. 4). *C. raciborskii* can potentially grow under nitrogen-limiting conditions owing to its ability to fix nitrogen (Moisander *et al.*, 2012; Figueredo *et al.*, 2014), but increasing the concentration of ammonium favors the dominance of non-nitrogen-fixing cyanobacteria (Blomqvist *et al.*, 1994; Branco and Senna, 1994). The mean ammonium concentration from June 2011 to December 2013 (2.41 μmol.L^{-1}) exceeded that from August 2009 to January 2011 (1.48 μmol.L^{-1}) (Yamamoto and Shiah, 2012), suggesting that the environment of the pond changed toward the direction that facilitates the growth of *M. aeruginosa*. *C. raciborskii* may have been outcompeted by *M. aeruginosa* in early summer 2011, and the absence of *C. raciborskii* might have favored the formation of a bloom of *M. aeruginosa* (see Branco and Senna, 1994). However, the absence or low abundance of *C. raciborskii* in the summers of 2012 and 2013 does not appear to be accounted for by the interference of *M. aeruginosa*, given the absence of *M. aeruginosa* blooms in these periods. The possibility that the growth of *C. raciborskii* in these summer seasons was controlled by cyanophages cannot be ruled out (Pollard and Young, 2010).

The fact that *C. raciborskii* continuously grew after its reappearance in the water suggests that the environmental conditions after late February 2012 were suitable for the growth of *C. raciborskii*. If the absence of *C. raciborskii* from August 2011 to mid-February 2012 was the result of unfavorable environmental conditions, *C. raciborskii* can be reasonably assumed to have been present in the bottom sediment in the form of akinetes during this period (Padisák, 2003; Rücker *et al.*, 2009). Akinete production is believed to be particularly important in the life cycle of Nostocalean cyanobacteria, enabling them to survive under adverse conditions. An increase in temperature triggers akinete germination, whereas the temperature at which *C. raciborskii* akinetes germinate varies among strains. The strain that was isolated from Lake Balaton showed a high percentage of germination only in the temperature range of 22–23.5 °C (Padisák, 1997). In contrast, based on the monitoring of akinete abundance in the sediment in Lake Melangsee, Rücker *et al.* (2009) concluded that akinete germination occurs at temperatures as low as 13 °C. The study pond experienced an unusually low temperature (13.9 °C) on 18 February 2012, but the water temperature returned to a normal level (18.4 °C) within a week, during which *C. raciborskii* trichomes appeared in the water. If the reappearance of *C. raciborskii* actually originated from the germination of akinetes, then release from 'cold stress' might have induced akinete germination. This supposition warrants further testing.

Although its abundance sometimes decreased below the detection limit in summer, *C. raciborskii* was almost continuously present in the water from its reappearance in late February 2012 until early May 2013. Notably, the seasonal dynamics of *C. raciborskii* during this period completely differed from those observed in a previous study that was conducted from August 2009 to January 2011 (Yamamoto and Shiah, 2012), which found that *C. raciborskii* abundance increased in summer and decreased in winter (Fig. 4). Yamamoto and Shiah (2014) showed that the two *C. raciborskii* strains that were isolated from the study pond in August 2009 and February 2012 differed greatly from each other in terms of growth, trichome size and akinete production, and they posited that these strains were different ecotypes that comprised the *C. raciborskii* population in the pond. A difference was also found between the specific growth rates of the strain that was tested in the present study and those isolated before (Yamamoto and Shiah, 2014), implying the presence of several ecotypes in the study pond. The possibility that the *C. raciborskii* that reappeared in late February 2012 was a different ecotype from that previously present would explain why *C. raciborskii* exhibited different seasonal patterns between the study periods, because the response to environmental conditions would vary among ecotypes (see Burford *et al.*, 2014).

In summary, this study showed that *C. raciborskii* grew in low-temperature seasons and disappeared in the summer months in a small artificial pond in northern Taiwan, even though it used to be a main component of summer blooms there. The abundance of *M. aeruginosa* has been increasing in recent years, and it formed a heavy bloom in the summer when *C. raciborskii* was absent from the water. Such a replacement of dominant cyanobacterial species was assumed to be caused by environmental changes, such as an increase in ammonium concentration. In addition, the possibility that *C. raciborskii* in the pond had been replaced by an ecotype that is more adaptable to low temperatures cannot be excluded.

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