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Thermal-dependent growth characteristics for Cylindrospermopsis raciborskii (Cyanoprokaryota) at different light availabilities: methodological considerations

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Abstract
Cylindrospermopsis raciborskii is one of the most common species of cyanobacteria that can cause nuisance blooms in tropical and subtropical waters. The spatial distribution of this species has become more widespread in temperate regions during the last decade. Sixty combinations of the interaction of light and temperature conditions were examined in this study to elucidate the growth dynamic of C. raciborskii ACT 9502 isolated from a temperate shallow lake (Lake Balaton, Hungary). The maximum growth rate of this strain was observed at 32.8 °C with 164 µmol m^{-2} s^{-1} of irradiance. C. raciborskii ACT 9502 was able to grow at both low and high temperatures if the irradiance was low, but could not tolerate the high irradiance at low temperatures. Low-temperature-induced photoinhibition was observed on higher irradiances with increasing temperature. Results here provide indirect evidence that with global warming, adaptation and high tolerance to a wide range of environmental factors, a harmful cyanobacteria can successfully expand to higher latitudes. The gradient experiment also demonstrated that the determination of temperature cardinals of growth and category of high light or shading tolerance significantly depend on the environmental irradiance and temperature. These are important parameters that must be considered when comparing global determinations of growth parameters of this invasive species.

Keywords
N_2-fixing cyanobacteria
Invasive species
Global warming
Interactive effect of light and temperature
Photoinhibition
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Introduction
Future climatic change scenarios predict rising temperatures (Ciscar et al. 2014), which can provide a catalyst for the global expansion of harmful cyanobacterial blooms (Paerl and Huisman 2008; Jöhnk et al. 2008; Paerl and Paul Huisman 2012). Cylindrospermopsis raciborskii is one of the most common toxic species of cyanobacteria that cause nuisance

blooms in tropical and subtropical waters (reviewed by Padisák 1997; Antunes et al. 2015), but this species has also been observed in temperate regions of Australia, Africa, Europe, and North and South America in recent years (Druart and Briand 2002; Wood and Stirling 2003; Shaker et al. 2003; Mischke, 2003; Bouaïcha and Nasri 2004; Hamilton et al. 2005; Stefaniak and Kokociński 2005 ; Stüken et al. 2006; Vidal and Kruk 2008; Stüken et al. 2006; Van Vuuren and Kriel 2008; Stefaniak and Kokociński 2005; Piccini et al. 2011). In newly invaded waters, C. raciborskii can form intense blooms after only a few years of its first appearance, particularly in warmer temperate regions. This negatively impacts the diversity of the natural algal assemblage and outcompetes the native species (Padisák et al. 1984; Chapman and Schelske 1997; Briand et al. 2002; Alster et al. 2010; Kovács et al. 2012). Knowledge of the optimal and suboptimal conditions for the growth of C. raciborskii is important to better understand the ecology and factors influencing its invasive characteristics. Temperature and light are considered to be the main physical factors that directly control the distribution and productivity of algae. The optimum temperature for the growth of a species is often different from the temperature at which the species can dominate in the field (Eppley 1972; Suzuki and Takahashi 1995; Tang et al. 1997). The dominance of an algal population is not expected to be solely temperature dependent. The effects of temperature or light have been extensively studied independently of each other (temperature effect at a single fixed irradiance and vice versa) (Tilman et al. 1981; Mur 1983; Ahlgren 1987; Thompson et al. 1992; Coesel and Wardenaar 1994; Sosik and Mitchell 1994; Kovács et al. 1997; Malinsky-Rushansky et al. 2002). However, these environmental factors coexist and jointly affect phytoplankton at the species and the community level in the natural environment. Some studies of diatoms, green algae and cyanobacteria demonstrate the importance of the interactions between temperature and light and focus the ecophysiological interest on these environmental factors (Graham et al. 1995; Albertano and Kováčik 1996; Ibelings 1996; Chaneva and Furnadzieva 1997; Popovich and Gayoso 1999; Latała and Misiewicz 2000). To date, there are no such data available in the literature concerning Cylindrospermopsis raciborskii. Some authors investigated the temperature effect at a single (fixed) irradiance and the influence of irradiance at a single (fixed) temperature for growth of strains of C. raciborskii originating from diverse areas (Shaker et al. 1999; Shafik et al. 2001; Briand et al. 2004, Chonudomkul et al. 2004; Piccini et al. 2011). However, the interaction of the range of light and temperature conditions on the growth of this invasive species is not described. The aim of this research is to fill this knowledge gap and describe the growth rates of C. raciborskii across gradients of interaction between temperature and light.

Methods

Strain, origin and their maintenance

Cylindrospermopsis raciborskii (Wołosz.) Seenayya and Subba Raju (ACT 9502) was isolated from Lake Balaton (Hungary, between 46°62′ and 47°04′N, and between 17°15′ and 18°10′E) in 1995. Lake Balaton is the largest shallow lake in central Europe, with a surface area of 596 km^2 and mean depth of 3.3 m. As in many temperate and tropical lakes, the eutrophication of Lake Balaton has been associated with an increasing dominance of cyanobacteria. From 1974 to the beginning of the 1990s, the mass development of filamentous cyanobacteria in summer became a regular phenomenon in the western and occasionally in the eastern part of the lake (Gorzó 1985; Vörös and Nagy Göde; 1993). The mean annual water temperature of the lake is 12.2 °C. The water temperature is normally above 20 °C from the end of May to early September, although during hot spells, temperatures of 28 °C are not unusual. The lake is exposed to strong winds (average 3.2 m s^{-1} over the year), which prevents pronounced thermal stratification. The average value of the light extinction coefficient (K_d) is 1.78 m^{-1} in the eastern portion of the lake, ranging from

0.62 to 3.68 m^{-1}. Suspended sediments tend to be the controlling factor for light extinction, which is strongly dependant on wave action. In the more eutrophic western part of the lake, the average K_d value is 3.31 m^{-1} owing to the abundance of algae, and the transparency is consequently low even in calm weather conditions (Herodek et al. 1988). After 1994, the biomass of algae decreased markedly as a result of implementing a range of management measures to decrease the phosphorous loading (Istvánovics 2008). However, N_2-fixing cyanobacteria remained dominant within summer phytoplankton blooms.
The isolated N_2-fixing C. raciborskii strains were maintained at 21 °C and 50 µmol m^{-2} s^{-1} in BG-11 medium (Rippka et al. 1979) with the following modifications: (1) sodium nitrate, the primary nitrogen source, was omitted to avoid morphological deformity, (2) iron (including the ammonium content) and phosphorous concentrations were halved to avoid precipitation, and (3) copper content of the medium was decreased to 0.02 mg l^{-1} ($CuSO_4 \cdot 5H_2O$) because C. raciborskii would not grow within the original Cu concentrations under isolation process.

Experimental conditions
C. raciborskii (ACT 9502) subsamples for inoculum were taken from a semi-continuous culture, which was operated at 23 °C on 80 µmol m^{-2} s^{-1}. Before starting the growth experiments, each inoculum was pre-incubated for at least two generations at temperature and irradiance of the treatment. Algae were incubated in autoclaved 500-ml Erlenmeyer flasks containing 150 ml of modified BG11 medium (see above) and plugged with a gauze and cotton stopper. All cultures were mixed at least four times a day. The growth experiments were started at low algal concentration (OD_{750} = 0.009–0.011, path length of cuvette 10 mm) to avoid the self-shading effect. Growth of the C. raciborskii treatments was determined in 60 combinations of temperatures (12, 15, 18, 21, 24, 27, 30, 33, 36 and 39 °C) and irradiances (10, 30, 60, 120, 230 and 390 µmol m^{-2} s^{-1}). The experiments were carried out in a water-filled black sidewall glass aquarium, divided into six compartments by five double-layered black partition walls. These walls included holes at the bottom to ensure the free flow of water for temperature regulation, while avoiding light penetration from adjacent compartments. Continuous illumination was provided from under the aquarium using cool white fluorescent tubes (20 tubes of Tungsram F33, 40 W). Irradiance was measured with a LI-190 SB 2π Quantum Sensor (LI-COR Inc., USA) in the centre of the bottom of the incubation bottles. To ensure precision of the temperature regulation, a refrigerated bath circulator was used (±0.1 °C, Neslab RTE 210). All treatments were conducted with three replicates.
Determination of growth parameters
Algal growth was monitored by measurement of optical density at 750 nm (OD_{750}) and 650 nm (OD_{650}) at the same time each day using a Shimadzu UV–VIS 160A spectrophotometer (Shimadzu Corporation, Japan). The growth curves determined by OD_{750} and OD_{650} were identical, and so specific growth rates of C. raciborskii in the cross-gradient experiments were calculated using absorbance at 750 nm. In the preliminary experiments, the growth estimates using optical density were found to be identical to those based on cell biomass determined by microscope counting (Fig. 1; Pearson's correlation coefficient, $r = 0.997$; $P < 0.001$).

Fig. 1
Correlation between the absorbance measured at 750 nm (OD_{750}) and the biomass of filaments of Cylindrospermopsis raciborskii (ACT 9502). The solid line is the regression through the data, and dashed lines are the 95 % confidence intervals
Maximum specific growth rates (
μ'maxµmax′

) for individual flasks were calculated for each of the 60 combinations of temperature and irradiance. The relationship between natural log OD_{750} and incubation time (day) was plotted, and regression lines were fitted (at least four points) to the linear portion of each curve (Guillard 1973). The slope of the line gave the

μ'max

(day^{-1}) for each flask.

Growth–irradiance relation

To estimate physiological parameters for the growth–irradiance relationship at different temperatures, a photoinhibition model was used as in Platt et al. (1980) with modifications to the photosynthetic rate for growth as in Ojala (1993):

$$\mu'\max=\mu_s\times(1-\exp(-\alpha\times E/\mu_s))\times\exp(-\beta\times E/\mu_s)$$

1

where

μ'max

(day^{-1}) is the observed maximum specific growth rate for an individual flask at E irradiance (μmol m^{-2} s^{-1}); μ_s (day^{-1}) is the theoretical maximum growth rate in the absence of any photoinhibition at optimal irradiance; α (day^{-1}(μmol m^{-2} s^{-1})$^{-1}$) is the light utilization efficiency for growth (the slope of the linear portion of the curve); β is the parameter characterizing photoinhibition.

The maximum growth rate (μ_{max}) at optimal irradiance (μ_{max}) (μmol m^{-2} s^{-1}) was calculated from the following equation (Platt et al. 1980):

$$\mu\max=\mu_s\times(\alpha/(\alpha+\beta))\times(\beta/(\alpha+\beta))^{\beta/\alpha}$$

2

The optimal irradiance for growth ($E_{m(\mu)}$, μmol m^{-2} s^{-1}) where the growth is maximum, the light saturation parameter for growth ($E_{k(\mu)}$, μmol m^{-2} s^{-1}) and the index of photoinhibition susceptibility for growth ($E_{b(\mu)}$, μmol m^{-2} s^{-1}), respectively, were calculated using the following equations:

$$E_{m(\mu)}=\mu_s/(\alpha\log_e((\alpha+\beta/\beta)))$$

3

$$E_{k(\mu)}=\mu\max/\alpha$$

4

$$E_{b(\mu)}=\mu_s/\beta$$

5

The parameters μ_s, α and β used in Eqs. 2, 3, 4, 5 are from Eq. 1, and μ_{max} is derived from Eq. 2.

Growth–temperature relation

To estimate physiological parameters for growth–temperature relationships throughout the entire temperature range, three alternative models commonly used by microbiologists were investigated.

1.

Parabolic model (Tang et al. 1997):

$$\mu\max=\mu_{opt}-\mu_{opt}((T_{opt}-T)^2/(0.5\times\Delta T)^2)$$

6

where μ_{max} (day^{-1}) is the maximum growth rate at optimal irradiance from the

μ'max

–E curve fitting at each temperature, μ_{opt} (day^{-1}) is the maximum specific growth rate throughout the entire temperature range, T_{opt} (°C) is the temperature at which $\mu_{max} = \mu_{opt}$, and ΔT (°C) is the range of temperature over which μ_{max} increases with T, experimental temperature (°C).

2.

Square root model (Ratkowsky et al. 1983):

$$\sqrt{\mu_{max}} = b \times (T - T_{min}) \times (1 - \exp(c \times (T - T_{max}))), \quad (7)$$

where μ_{max} (day^{-1}) is the same as in Eq. 6, T (Kelvin, K) is the experimental temperature, T_{min} and T_{max} (K) are the minimum and maximum temperatures, respectively, at which the growth rate is zero. The parameter b is the regression coefficient of the square root of growth rate constant versus degrees Kelvin for temperatures below the optimal temperature, whereas c is an additional constant to enable the model to fit the data for temperatures above the optimal temperature.

3. Cardinal temperature model with inflection, CTMI (Rosso et al. 1993):

$$\mu(T) = \mu_{max} \times \frac{(T - T_{min})^2 \times (T - T_{max})}{(T_{opt} - T_{min}) \times [(T_{opt} - T_{min}) \times (T - T_{opt}) - (T_{opt} - T_{max}) \times (T_{opt} + T_{min} - 2T)]}, \quad (8)$$

where μ_{max} (day^{-1}), T, T_{min} and T_{max} (°C) are the same as in Eq. 7, and T_{opt} (°C) is the optimal temperature of growth at which $\mu = \mu_{max}$.

The activation energy of rate-limiting steps for growth as a function of temperature was determined by employing the logarithmic version of the Arrhenius equation (Kruger and Eloff 1978).

Determination of filament abundance and biovolume

Filaments of C. raciborskii were counted by an inverted microscope. A minimum of 400 filaments were counted in each sample, with a typical counting error of 10 % (95 % confidence limits; Lund et al. 1958). The total biovolume of the filaments was calculated from the abundances, and the length and the diameter of filaments were obtained by measuring 30 randomly selected individuals (Hillebrand et al. 1999). The biomass (wet weight) of filaments was estimated from the total volume assuming a specific gravity of 1.0.

Statistical analysis

Fitting the Platt model (Platt et al. 1980) to the experimental data (μ_{max}–E) was done by nonlinear least squares fitting method based on the Levenberg–Marquardt algorithm. The data were unweighted. Temperatures at which there was no detectable growth at any irradiances (12 and 39 °C) were excluded from the curve fitting. The maximum specific growth rates of triplicates grown at different irradiances and temperatures were compared for significance among treatments (light, temperature, their interaction) with a two-way analysis of variance (ANOVA). Significance level was set at $P < 0.05$. The Shapiro–Wilk test was performed to assess the normality of maximum growth rates. At the 0.05 level, the data were significantly drawn from a normally distributed population. Pearson's correlation analyses, curve fittings, statistics and graphical plotting were performed using the OriginPro 8.6.0 software package (OriginLab Corporation, USA).

Results

Temperature dependence of growth of C. raciborskii at optimal light condition

The minimum and maximum temperatures at which growth of C. raciborskii strain ACT9502 was observed in the experiments were 12 and 36 °C, respectively. The maximum growth rate was lowest (0.13 day^{-1}) at 12 °C (Fig. 2a), and its values increased with temperature up to 33 °C where μ_{max} (0.81 day^{-1}) was observed (Fig. 2c). Above 33 °C, there was an increasing tendency of maximum growth rate turnover, while at 39 °C the cells did not grow and the inoculum died.

Fig. 2

Maximum specific growth rates (

μ'maxμmax′

) of Cylindrospermopsis raciborskii (ACT 9502) as a function of irradiance at 15, 18, 21 and 24 °C (a), at 27 and 30 °C (b), at 33 and 36 °C (c). The lines show the μ–E I curves fitted to the replicates by Platt et al. (1980) model. The fitting statistics are given in Table 1

The growth–temperature relationship of C. raciborskii strain ACT9502 showed a linear correlation within two sections of the suboptimal temperature range (Fig. 3a):

Fig. 3

Estimated physiological parameters for growth–irradiance relationship of Cylindrospermopsis raciborskii (ACT 9502) at different temperatures used by Platt et al. (1980) model; a μ_{max}, the maximum growth rate at optimal irradiance at a particular temperature; as a consequence of the impossibility of fitting at 12 °C, each

μ'maxμmax′

value of the triplicate was represented; b $E_{b(\mu)}$, the index of photoinhibition susceptibility for growth; c $E_{m(\mu)}$, the optimal irradiance for growth; d $E_{k(\mu)}$, the light saturation parameter for growth; e the T_{opt} for growth of Cylindrospermopsis raciborskii (ACT 9502) at different irradiances

(i)

at temperatures ranging from 12 to 24 °C ($\mu_{max} = 0.046 \times T - 0.428$, $r = 0.994$, $P < 0.001$);

(ii)

at temperatures ranging from 24 to 33 °C ($\mu_{max} = 0.014 \times T + 0.335$, $r = 0.980$, $P < 0.01$).

The inflection point between lines was 24 °C. The activation energy for growth of C. raciborskii ACT 9502 as a function of temperature was 71.8 and 16.52 kJ mol^{-1} below and above the inflection point, respectively.

Throughout the entire temperature range, the parabolic function (Eq. 6) did not provide a good fit for the relationship between light-saturated maximum specific growth rates and temperature for C. raciborskii ACT 9502 (Fig. 4a). The change in growth with temperature was not symmetrical around T_{opt}. However, the square root (Eq. 7) and CTMI (Eq. 8) models provided adequate fit for the growth–temperature relationship of this strain (Fig. 4b, c). Fitting showed that the C. raciborskii strain 9502 isolated from a temperate lake had a high-temperature optimum for growth (32.8 °C). The T_{opt} was only a few degrees below the T_{max}, above which no growth occurs. The T_{mins} of −2.2 and −3.2 °C as determined by CTMI and square-root models, respectively, was unrealistically low.

Fig. 4

Estimated physiological parameters for the growth–temperature relationship of Cylindrospermopsis raciborskii (ACT 9502) by a Pp arabola function model, b cardinal temperature model, c square-root model over the entire temperature range

Interaction effect of light and temperature on growth of C. raciborskii

The effects of temperature, light and their interaction were significant on the growth of C. raciborskii ACT9502 strain (Table 1). The characteristics of growth rate versus irradiance (

μ'maxμmax′

–E) curves changed markedly with temperature (Fig. 2; Table 2). Three types of

μ'maxμmax′

–E curves were distinguished:

Table 1

Two-way ANOVA for maximum specific growth rate (

μ'maxμmax′

) of Cylindrospermopsis raciborskii (ACT 9502) as a function of temperature and irradiance

Sources of variation	**df**	**Ss**	**Mss**	**F values**
Temperature	7	2.841	0.406	560.85***

Table 1
Two-way ANOVA for maximum specific growth rate (μ'max μmax′) of Cylindrospermopsis raciborskii (ACT 9502) as a function of temperature and irradiance

Sources of variation	**df**	**Ss**	**Mss**	**F values**
Irradiance	5	4.045	0.809	1117.88***
Interaction	35	2.090	0.060	82.52***
Model	47	8.976	0.191	263.90***
Error	96	0.070	7.236E−4	–
Corrected total	143	9.045	–	–

Df degrees of freedom, Ss sum of squares, Mss mean square, F values Fisher F test statistic

*** P value < 0.001

Table 2
Growth parameters of Cylindrospermopsis raciborskii (ACT 9502) calculated using the Platt et al. (1980) model at different temperatures and a curve-fitting statistic

Temperature	**μ_s**	**α**	**β**	**Fitting statistics**		
(°C)	**(day^{-1})**	**(day^{-1}(μmol m^{-2} s^{-1})$^{-1}$)**	**(day^{-1}(μmol m^{-2} s^{-1})$^{-1}$)**	**Reduced Chi-sqr**	**Adj. R^2**	**P value**
15	0.354 (0.038)	0.0363 (0.0073)	0.0022 (5.999E−4)	0.0014	0.490	<0.001
18	0.437 (0.030)	0.0174 (0.0017)	9.448E−4 (2.047E−4)	0.00074	0.895	<0.001
21	0.609 (0.035)	0.0190 (0.0014)	7.299E−4 (1.764E−4)	0.00092	0.951	<0.001
24	0.759 (0.037)	0.0184 (9.705E−4)	4.476E−4 (1.489E−4)	0.00081	0.977	<0.001
27	0.752 (0.020)	0.0203 (6.934E−4)	1.533E−4 (7.461E−5)	0.00035	0.992	<0.001
30	0.782 (0.064)	0.0187 (0.0017)	1.581E−4 (2.283E−4)	0.00279	0.953	<0.001
33	1.137 (0.236)	0.0167 (0.0020)	0.00148 (0.00102)	0.00708	0.919	<0.001
36	1.500	0.0150 (0.0011)	0.00409 (2.7541E−4)	0.00699	0.926	<0.001

Table 1
Two-way ANOVA for maximum specific growth rate (μ'maxμmax′) of Cylindrospermopsis raciborskii (ACT 9502) as a function of temperature and irradiance

Sources of variation	df	Ss	Mss	F values
	(0.000)			

±SE for the regression estimate of each parameter is given in parentheses

μ_s (day^{-1}), theoretical maximum growth rate in the absence of any photoinhibition at optimal irradiance; α (day^{-1}(μmol m^{-2} s^{-1})$^{-1}$), the light utilization efficiency for growth (the slope of the linear portion of the curve); β, the parameter characterizing the photoinhibition

(i)
At low temperatures, the light requirement of C. raciborskii was low and photoinhibition of growth appeared with low irradiance (Figs. 2a, 3b). At 12 °C, growth was observed only at the lowest irradiance (10 μmol m^{-2} s^{-1}), while the inoculum died at higher irradiances. At 15 °C, growth was observable at every irradiance except 390 μmol m^{-2} s^{-1}, but was strongly inhibited by light above 30 μmol m^{-2} s^{-1}. With increasing temperature (18, 21 and 24 °C), the photoinhibition of growth appeared at higher irradiances (>60 μmol m^{-2} s^{-1}, >120 μmol m^{-2} s^{-1}, >230 μmol m^{-2} s^{-1}, respectively), and the inhibition effect became weaker. At 24 °C, photoinhibition almost disappeared.
(ii)
At 27 and 30 °C, growth reached the light saturation at 230 μmol m^{-2} s^{-1} and was not inhibited by the highest irradiance applied (390 μmol m^{-2} s^{-1}; Figs. 2b, 3b).
(iii)
At high temperatures (33 and 36 °C), the photoinhibition reappeared above 230 and 120 μmol m^{-2} s^{-1}, respectively, and became stronger with increasing temperature (Figs. 2c, 3b).
The photoinhibition property of the μ_{max}–E curve at different temperatures was well quantified by the index of photoinhibition susceptibility ($E_{b(\mu)}$) (Fig. 3b). $E_{b(\mu)}$ values increased with decreasing photoinhibition from 15 to 27 °C. Above 30 °C, its value decreased parallel with photoinhibition. The optimal irradiance for growth ($E_{m(\mu)}$) of C. raciborskii ACT 9502 strain increased with temperature and saturated around 150–200 μmol m^{-2} s^{-1} above 24 °C (Fig. 3c). The light saturation parameter for growth ($E_{k(\mu)}$) was positively correlated with temperature (in the range of 15–36 °C; $E_{k(\mu)} = 1.895 \times T - 14.77$, $r = 0.966$, $P < 0.0001$) (Fig. 3d). However, the light utilization efficiency ($\alpha_{(\mu)}$) showed little change with temperature, with the exception of 15 °C (Table 2). The T_{opt} for growth increased sharply at low irradiances and showed a saturated function above 60 μmol m^{-2} s^{-1} (Fig. 3e).

Discussion

Temperature dependence of growth at optimal light condition

Population growth is an integrated metabolic parameter, representing the sum of many chemical and physical processes with a strong dependence on temperature. For many phytoplankton species, the relationship between temperature and specific growth rate is either exponential (Eppley 1972; Li and Morris 1982; Thompson et al. 1992) or linear over a relatively large range of temperatures (Rhee and Gotham 1981; Sosik and Mitchell 1994; Montagnes et al. 2003). The square root of μ_{max} for C. raciborskii ACT 9502 is linear with temperature in the suboptimal range. However, an abrupt decrease of μ_{max} was observed from

the optimal temperature to the maximum temperature for growth, as also observed for most bacteria (Ratkowsky et al. 1982; Zwietering et al. 1991). The activation energy for growth of C. raciborskii 9502 under the inflection point is much higher (71.8 kJ mol^{-1}) than above 24 °C (16.52 kJ mol^{-1}). In Lake Balaton, C. raciborskii proliferation and blooms were observed generally above 24 °C. Kruger and Eloff (1978) determined that the inflection point of a temperature–growth curve for Microcystis cyanobacteria correlated well with initiation of blooms for this taxon.

Temperature-dependent physiological properties of different algal species have an influence on the community composition of phytoplankton and their geographical distribution. With increasing temperature, the highest growth rates for phytoplankton groups increased from diatoms, via green algae to cyanobacteria (Canale and Vogel 1974; Paerl and Huisman 2009). Our fitting for the entire temperature range shows that the C. raciborskii strain 9502 has a high T_{opt} for growth (32.8 °C). During the largest blooms in Lake Balaton (1982, 1992 and 1994), the summer water temperatures were above 26 °C and sometime reached 29 °C, and the contribution of C. raciborskii to the total phytoplankton biomass was in excess of 90 % (Padisák et al. 1984; Présing et al. 1996). There have been many other reports of C. raciborskii blooms and dominance (70–90 % contribution) associated with high water temperatures: Fitzroy river, Australia 27.1–29.5 °C (Fabbro and Duivenvoorden 1996); local ponds of City Varanasi, India, 28–30 °C (Singh 1962); Paranoá reservoir, Brazil, 24–28 °C (Branco and Senna 1994); 47 reservoirs and weir pools across tropical and subtropical Queensland, Australia, 28–32 °C (McGregor and Fabbro 2000); and Lake Kinneret, Israel, 29–30 °C (Alster et al. 2010).

Average water temperatures decrease towards higher latitudes in the northern and southern hemispheres of temperate regions, and the expansion of C. raciborskii to higher latitudes was observed near the end of the twentieth century (Mischke 2003; Stefaniak and Kokociński 2005; Stüken et al. 2006; Wiedner et al. 2007; Kokociński et al. 2010; Kokociński and Soininen 2012). Generally, this species does not dominate or cause serious blooms in colder temperate regions (the contribution to the algal assemblages is ~10–20 %). Although Dokulil and Mayer (1996) reported that after C. raciborskii was first recorded in a shallow urban lake (Alte Donau, Austria), it quickly became the main algal species, contributing up to 90 % of the total phytoplankton biovolume at 15–18 °C. Our results support other physiological studies (Chonudomkul et al. 2004; Wiedner et al. 2007) that showed the lower limit of C. raciborskii growth was 10–12 °C. However, the presence of C. raciborskii filaments has been observed below 10 °C in Lake Balaton in winter (personal communication of E. Takáts and I. Kóbor), when normally C. raciborskii overwinters as an akinete in the sediment of this lake (Gorzó 1987; Kovács et al. 2003). Vegetative winter survival of C. raciborskii was also observed around this temperature in other regions (Dokulil 2015).

T_{opt} for growth of cyanobacteria can be significantly higher than the temperature of their native habitats (Tang et al. 1997). Measurements proved that the T_{opt} for growth of the strains of C. raciborskii isolated at different locations in Europe and around the world are between 27.8 and 35 °C (this study; Chonudomkul et al. 2004; Briand et al. 2004; Mehnert et al. 2010). However, C. raciborskii has a broad tolerance to a range of environmental temperatures, which may explain its ability to spread towards the higher latitudes. The large surveys started for monitoring of lakes (latitude 50°–55° in northern hemisphere) in the last decade verified the presence of C. raciborskii more widely than previously thought (Stüken et al. 2006; Kokociński and Soininen 2012). This raises the question as to why northern populations of C. raciborskii started to spread north only within the last decades and not earlier? It is worth noting that the exact time this species first entered the susceptible lakes is unknown. The sediment can be seen as a “resting seed bank” in which different types of surviving algal cells accumulate for long periods (even years or decades, Livingstone and Jaworski 1980) until

favourable conditions for germination occur in the water. Germination studies have shown that survival cells of "hidden" species (for example, Anabaena compacta and Anabaenopsis cunningtonii in Lake Balaton) exist in the sediment before their vegetative filaments can be observed in the lake water (Padisák and Kovács 1997; Kovács et al. 2012).

Interaction effect of light and temperature on growth of C. raciborskii

Numerous data on the specific growth rates of algae in culture have been assembled (Hoogenhout and Amesz 1965; Eppley 1972; Thompson et al. 1992; Suzuki and Takahashi 1995; Shafik et al. 2001; Briand et al. 2004; Piccini et al. 2011). However, the highest growth rates of the studied species were determined only at a single irradiance or temperature. Our results indicate that the growth of C. raciborskii at temperatures (which principally reflects photosynthesis) depends significantly on the amount of light available. As suggested by Robarts and Zohary (1987), experiments carried out under subsaturating irradiances do not reveal the light-saturated temperature responses and are incomparable with other data. Our results corroborate this conclusion and differ from the results of Briand et al. (2004), who determined the T_{opt} for growth of ten strains of C. raciborskii at low, subsaturating irradiance (30 μmol m^{-2} s^{-1}). Their growth results showed that the optimal temperatures of these strains from tropic and temperate regions were almost the same (T_{opt} ranged from 29 to 31 °C, according to the CTMI equation) and did not show any trend concerning geographical origin. However, the authors demonstrated also that differences in light sensitivity among these strains were noticeable. Our results indicate that the relationship between T_{opt} and irradiance is important for growth (6 °C difference of T_{opt} determined at optimal and suboptimal lighting). Presumably, the T_{opt} of ten C. raciborskii strains from tropical and temperate regions would show more characteristic differences if determined at saturating irradiance.

At low temperature, low and high light condition

Although the initial photochemical reactions are independent of temperature, many associated reactions of photosynthesis are temperature dependent (Raven and Geider 1988). High levels of photosynthetically available radiation have been shown to inhibit photosynthesis (Öquist et al. 1987). It is well established that the susceptibility of photosynthesis to photoinhibition increases at low temperatures; this phenomenon is called low-temperature-induced photoinhibition (Öquist 1983; Long et al. 1994). According to our results, the inhibition irradiances for growth of C. raciborskii were very low (between 12 and 21 °C) and with increasing temperature shifted to higher irradiances. This physiological phenomenon should be kept in mind in the planning of experiments and explanation of results. Mehnert et al. (2010) showed that the native cyanobacteria grew at rates of 0.06–0.15 day^{-1}, whereas invasive cyanobacteria (including C. raciborskii isolated from Werbellinsee, Germany) did not grow at 10 °C. Lower growth rates for invasive cyanobacteria were also reported compared to native ones (around 0.12 and 0.32 day^{-1}) at 15 °C, suggesting that the native species were better competitors at low temperatures in some German lakes. However, the authors determined the temperature dependence of growth at a single irradiance (80 μmol m^{-2} s^{-1}). Our results demonstrated that the growth of C. raciborskii is strongly dependent on the applied irradiance at low temperatures. At 15 °C, the growth rate of C. raciborskii 9502 (0.15–0.2 day^{-1} on 80 μmol m^{-2} s^{-1}) coincided very well with values reported for the German strain, but the growth potential was more than 70 % higher (0.32 day^{-1}) measured at lower irradiance (30 μmol m^{-2} s^{-1}).

High temperature and high light condition

Above 30 °C, the light inhibition for growth of C. raciborskii ACT 9502 reoccurred, and the inhibition became stronger with increasing temperature. Ibelings (1996) showed similar results. Irradiances that were sufficient to induce photoinhibition could cause greater damage in Anabaena flos-aquae (cyanobacteria), when combined with increased temperature. In contrast, the results of Jensen and Knutsen (1993) with Spirulina platensis (cyanobacteria) and

Wünschmann and Brand's (1992) studies with Synechoccocus sp. (cyanobacteria) showed that photoinhibition decreases with increasing temperature.

High temperature and low light condition

At high temperatures, the maintenance energy requirement increases parallel with respiration. Graham et al. (1995) reported that the respiratory losses of the filamentous green alga Spirogyra exceeded the photosynthetic carbon incorporation at low irradiances and high temperatures. A similar phenomenon was observed in our experiments. At 30 μmol m^{-2} s^{-1}, the

μ'maxμmax′

of C. raciborskii decreased with increasing temperature, while at 10 μmol m^{-2} s^{-1} cells died (after inoculation) at both 33 and 36 °C.

According to our results, C. raciborskii was able to grow with low irradiance at any temperature (low and high), but could not tolerate high irradiance at low temperatures. This physiological property might explain its seasonal dynamics in nature. In Lake Balaton, the appearance and success of C. raciborskii were typical in mid- or late summer when the water temperature was high (22–28 °C) and the available light was relatively low ($Z_m/Z_{eu} > 2$). However, in contrast to other N_2-fixers (Aphanizomenon sp., Anabaena sp.) C. raciborskii was generally absent in late spring or early summer when high irradiance (higher transparency, $Z_m/Z_{eu} < 2$) was associated with low temperature. In some years, filaments of C. raciborskii appeared in early summer, but proliferated more vigorously in late summer. Apparently, the species-specific temperature dependence of germination contributes to the species succession. The temperature dependence for germination of C. raciborskii showed a unimodal optimum curve with a narrower range of optimum temperatures (22.3–24.0 °C) compared to other N_2-fixers (Gorzó 1986; Kovács et al. 2012). However, based on results from Gorzó (1986), it must be noted that the germination of akinetes of C. raciborskii can start from 16 °C and slowly accelerate up to 22.3 °C, where the germination process in time reaches the optimum temperature.

C. raciborskii has been regarded as a superior competitor in the successional pathway of N_2-fixers in other lake systems. Pierangelini et al. (2015) showed the capability of C. raciborskii NPD to maintain photosynthesis by using the simple and low-cost mechanism of changes in antenna size. This could define its ability to grow and compete with other microalgae in the final stages of HABs, where light is relatively low and stable. These observations suggest that C. raciborskii can tolerate self-shading more effectively than other N_2-fixing filamentous cyanobacteria. The $I_{k(\mu)}$ values for growth of C. raciborskii 9502 were very low and showed strong temperature dependence (varied from 7.7 to 52 with increasing temperature). Padisák and Reynolds (1998) proposed a specific assemblage for C. raciborskii (Sn) based on its shade tolerance, which is different from other heterocitic cyanobacteria. In germination experiments with akinetes from fresh sediment of Lake Balaton, Kovács et al. (2012) clearly showed that C. raciborskii outcompeted other N_2-fixing cyanobacteria at low irradiance (30 μmol m^{-2} s^{-1}), but gradually lose dominance with the increase in light availability. Results from microcosm experiments using isolated strains from German lakes found that the strongest competitors were Aphanizomenon aphanizomenoides, followed by C. raciborskii and then other native and invasive N_2-fixers (Mehnert et al. 2010). However, the authors noted that the high growth rate of A. aphanizomenoides in the laboratory was contradictory to its low abundance in the field. Mehnert et al. (2010) used a phosphorous-rich complete Z8 medium for the mesocosm experiment, which may explain the difference in behaviour. In the germination and growth experiments of Kovács et al. (2012), the N_2-fixing cyanobacteria showed a very different contribution pattern depending on the initial phosphorous concentration. In the "P-enriched" variant (5600 μg l^{-1} PO_4–P), C. raciborskii was dominant (47–56 % of the total biovolume) at the beginning of the experiment at the lowest irradiance (30 μmol m^{-2} s^{-1}), but its

contribution to the N_2-fixer assemblages decreased to 12 % towards the end of the experiment (15th day). From the 9th day, A. aphanizomenoides became dominant independent of irradiance, in contrast to the results of the phosphorous-poor variant (close to natural condition) where its contribution to the algal assemblage was <20 %.

To explain the spread of C. raciborskii to mid-latitudes, three different hypotheses have been suggested: (1) high phenotypic plasticity; the species has ability to tolerate a wide range of climatic conditions, (2) global warming; climatic change increases water temperatures and allows species of tropical and subtropical origin to spread to temperate habitats and (3) ecotypes selection; adaptation to variations of habitat and existence of different ecotypes with different fitness. Our results conclude that high physiological tolerance of C. raciborskii may enable it to grow in a wide range of environmental conditions. At the same time, the high T_{opt} for growth of C. raciborskii is an advantage with the progressive warming of temperate water bodies. The increase in water temperature, driven by the change in climate, is systematically shifting the start date of germination earlier in the year, resulting in a prolonged proliferation period for N_2-fixers and shifting the pelagic population into a phase with higher light intensity (Wiedner et al. 2007). The higher light conditions accelerate germination and provide higher amount of inoculum for planktonic life (Kovács et al. 2012). In line with this, the comparison of our results with the experiments of Mehnert et al. (2010) indicate that the C. raciborskii strain isolated from German lakes can show cold adaptation. The T_{opt} of the German strain was 4.97 °C lower than the Hungarian one. This difference was also observed in the water temperature at which C. raciborskii appeared in Werbellinsee (17 °C) and in Lake Balaton (21–22 °C). The cold adaptation could indicate that the Hungarian isolate is inhibited by light at low temperatures, while the German variant is not.

In conclusion, our results provide indirect evidence that with global warming, adaptation and high tolerance to a wide range of environmental factors, C. raciborskii, a harmful cyanobacteria, can successfully expand to higher latitudes. This gradient experiment clearly demonstrates that the determination of the temperature cardinals of growth and category of high light or shading tolerance significantly depend on the environmental irradiance and temperature, respectively. This fact should be kept in mind when comparing global determinations of growth parameters of this invasive species.

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