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8 Photosynthetic characteristics of the benthic diatom species *Nitzschia frustulum* (Kützing)  
9 Grunow isolated from a soda pan along temperature-, sulphate- and chloride gradients

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20

## 21 **Abstract**

22 The Carpathian basin hosts a number of small, shallow, saline, alkaline ponds. As being  
23 endorheic basins, they are highly threatened by the climate change and response of biota to  
24 changing climate has been largely unexplored. We investigated the effects of salinity changes  
25 on the photosynthetic activity of *Nitzschia frustulum*, which is one of the main dominant taxa  
26 of the saline lakes in the Fertő-Hanság Region of the Carpathian basin. The photosynthetic  
27 activity of the species was measured along temperature (5, 10, 15, 20, 25, 30, 35, 40 °C), light  
28 (0 - 8 - 35 - 70 - 110 - 200 - 400 - 800 - 1200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $\text{SO}_4^{2-}$  (0 - 50 - 600 - 1200 - 2400 -  
29 3600 - 4800  $\text{mg L}^{-1}$ ) and  $\text{Cl}^-$  (0 - 36 - 437.5 - 875 - 1750 - 3500 - 5250  $\text{mg L}^{-1}$ ) gradients under  
30 laboratory conditions in photosynthetron. The conductivity optimal of *N. frustulum* was  
31 around 5600  $\mu\text{S cm}^{-1}$  with wide salinity tolerance. The species preferred the  $\text{HCO}_3^-$  -  $\text{SO}_4^{2-}$   
32 type waters since its photosynthetic activity (3.62  $\text{mgC mgChl-}a^{-1} \text{h}^{-1}$ ) was more than twice  
33 higher than in  $\text{HCO}_3^-$  -  $\text{Cl}^-$  type media. Its photosynthesis saturated at very low light intensity  
34 and photoinhibition was not observed during the experiments. The maximal photosynthesis

35 was measured at 28-29 °C. However, above 30 °C the decline of photosynthesis of *N.*  
36 *frustulum* can be forecasted.

37

38 **Keywords:** *Nitzschia frustulum*, photosynthetic activity, salinity, temperature, light, saline  
39 lakes

## 40 **Introduction**

41 Most climate change models (Christensen and Christensen 2007; George et al. 2007) predict  
42 substantial changes in hydrological balance and ecological functioning in both rivers and  
43 lakes (Jarman and Jones 1982) projecting increasing summer temperatures, decreasing  
44 groundwater level and annual precipitation, changes in the duration of the ice-free period and  
45 stratification patterns of the lakes (Dokulil 2013). These models also predict decreasing water  
46 levels and a reduction of wetland areas (Dokulil 2013) as a consequence of misbalance in the  
47 hydrological regimes (Williams 1981; Hammer et al. 1983; Fritz et al. 1993; Mason et al.  
48 1994).

49 Endorheic shallow saline lakes can be found on all continents (Bauld 1981; Hammer  
50 1986; Goudie 2003; Williams 2005; Boros et al. 2006). They are highly influenced by climate  
51 variables since their water level (practically: their existence) largely depends on the  
52 evaporation and rainfalls. Changes caused by the climate change cascade to their chemical  
53 and physical variables, and their flora and fauna (Wilhelm et al. 2006; Dokulil 2013). Climate  
54 was demonstrated to be an important predictor of zooplankton biomass, community  
55 composition and food-web dynamics (Gyllström et al. 2005); it may change overall  
56 abundance and community composition of bacteria and fungi (Castro et al. 2010), cladocerans  
57 (Molinero et al. 2007), marine and estuarine fish (Roessig et al. 2004) and algal assemblages  
58 (Harley et al. 2006; Anneville et al. 2015).

59 Soda pans are extreme habitats having special chemical and physical features. They  
60 are characterized by high levels of conductivity, day-night temperature variation, turbidity,  
61 pH, alkalinity and TP (total phosphorus) concentration (Boros et al. 2014; Stenger-Kovács et  
62 al. 2014). These features impose multiple stress on their biota (Pálffy et al. 2014), which may  
63 intensify with climate change (Caldeira and Wickett 2003). Such aquatic habitats occur in  
64 Central Europe (Keresztes et al. 2012; Horváth et al. 2013; Somogyi et al. 2014) especially in  
65 two regions of Hungary and Austria: the Danube-Tisza Interfluve and the Fertő-Hanság  
66 region (Stenger-Kovács et al. 2014). The lakes in these two regions have somewhat different  
67 chemical and physical features (Boros et al. 2014; Stenger-Kovács et al. 2014): all have high  
68  $\text{HCO}_3^-$  concentration, but in the Fertő-Hanság region  $\text{SO}_4^{2-}$  is the co-dominant anion and in the  
69 Danube-Tisza Interfluve  $\text{Cl}^-$ .

70 Diatom communities have been widely used to assess long-term changes in lakes due  
71 to the shift in climate (Smol 1991). According to the paleolimnological studies, diatom  
72 species distributions are highly correlated with salinity and the anion composition ( Servant-

73 Vildary and Roux 1990; Roux et al. 1991; Blinn 1993; Cumming and Smol 1993; Gasse et al.  
74 1995; Wilson et al. 1994), however, the underlying ecophysiological processes have been  
75 unknown (Saros and Fritz 2002). Salinity, temperature, pH and conductivity have both direct  
76 and indirect effects on the composition and biomass of phytoplankton and phytobenthos  
77 (Sullivan and Currin 2000; Hasegawa et al. 2000; Munns 2002; Sudhir and Murthy 2004).  
78 Diatoms are a major group of photoautotrophic organisms in alkaline saline lakes (Servant  
79 Vildary 1984; De Deckker 1988; Ionescu et al. 1998) similar to oceans (Mann 1999; Nelson  
80 et al. 1995; Sarthou et al. 2005).

81 The bulk of the photosynthetic measurements were carried out with phytoplankton  
82 species, mainly fast-growing species easy to culture (Stramski et al. 2002; Radchenko and  
83 Il'Yash 2006; Sobrino and Neale 2007; Roubex and Lancelot 2008) and only along  
84 temperature, irradiance and NaCl gradients (Pinckney and Zingmark 1991; Brotas and  
85 Catarino 1995). No photosynthetic rate measurements are available on species preferring in  
86 lakes with high  $\text{HCO}_3^-$  and  $\text{SO}_4^{2-}$  concentrations. One of the dominant benthic diatom in the  
87 soda pans of the Carpathian basin is *Nitzschia frustulum*. Its dominance within the diatom  
88 assemblage is typically higher than 10% in pans where the conductivity (mean: 5300; min:  
89 1410; max: 13650  $\mu\text{S cm}^{-2}$ ), temperature (mean: 25; min:13; max: 35°C), light irradiance  
90 (mean: 490; min: 20; max: 1600  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and  $\text{SO}_4^{2-}$  concentration (mean: 604; min: 26;  
91 max: 2433  $\text{mg L}^{-1}$ ) was relatively high, and  $\text{Cl}^-$  was relatively low (mean: 94; min: 4; max:  
92 575  $\text{mg L}^{-1}$ ) (Stenger-Kovács et al. 2014).

93 The projected effect of climate change in endorheic lakes includes raise in the ionic  
94 concentrations as a consequence of increasing air temperature and evaporation parallel with  
95 decreasing amount of precipitation. In the soda pans in this study, sulphate, chloride  
96 (consequently: conductivity) and water temperature will increase, and because of a decrease  
97 in water level, light availability will increase accordingly.

98 In this study, a culture of *N. frustulum* was used to explore ecophysiological effects of  
99 the changes expectable according to climate change models. We hypothesize that (i) the  
100 photosynthetic activity of *Nitzschia frustulum* will be higher in  $\text{SO}_4^{2-}$  than in  $\text{Cl}^-$  dominated  
101 media. We suppose that (ii) *Nitzschia frustulum* needs at least medium irradiance to optimize  
102 its photosynthesis, (iii) while at high light intensities photoinhibition will occur. The species  
103 is assumed (iv) to tolerate higher temperatures. Based on the photosynthetic characteristics of  
104 the species, (v) *Nitzschia frustulum* will be a beneficiary of the environmental conditions set  
105 by climate change in soda pans. To support or reject these hypotheses, photosynthetic activity

106 of the species was measured along temperature, light,  $\text{SO}_4^{2-}$  and  $\text{Cl}^-$  gradients using an *in vitro*  
107 device and monoclonal cultures.

## 108 **Material and methods**

### 109 *The sampling site, physical and chemical features of the lake*

110 *Nitzschia frustulum* was isolated from the Borsodi-dűlő (N 47° 06,815', E 16° 84,000'; 170  
111 m), which is a small, shallow, saline inland lake situated in the Fertő-Hanság National Park.  
112 The average chemical and physical features based on monthly collected and analyzed data  
113 during 2012 are summarized in Table 1. The lake is alkaline (mean pH ~ 9), well oxygenated  
114 (mean DO% ~94%) occasionally with extreme oxygen saturation values (18.1% - 197.2%).  
115 An increase in conductivity values was a regularly detected before the dry periods (summer),  
116 and the maximum reached 8150  $\mu\text{S cm}^{-1}$  in 2012. The lake is rich in nutrients such as SRP  
117 (soluble reactive phosphorus) and nitrogen forms due to droppings of waterfowl and  
118 mammals (Horváth et al. 2013; Stenger-Kovács et al. 2014). According to the anion and  
119 cation composition of the lake, it can be classified as one of the subtype of the alkaline saline  
120 inland waters (Hammer 1986; Grant 2006; Warren 2006) dominated by  $\text{Na}^+$ ,  $\text{Mg}^{2+}$ ,  $\text{HCO}_3^-$   
121 and  $\text{SO}_4^{2-}$  ions. The lake is moderately colored by humic materials (mean color ~ 32 mg Pt<sup>-1</sup>)  
122 with medium light availability. The turbidity ranged between 30 and 1320 FNU (average  
123 407.7 FNU), and the annual average light intensity measured directly above the benthos was  
124 600  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .

### 125 *The culture*

126 *Nitzschia frustulum* was isolated on 20th January in 2012 using a micromanipulator  
127 (Narishige) and one-cell isolation method under a light microscope (Zeiss, Axio Invert 40 C).  
128 The species was identified in light microscope (Trobajo et al. 2012) and subsequent  
129 investigations with a scanning electron microscope (Hitachi S-2600N) supported it as  
130 *Nitzschia frustulum* (Fig. 1). The species was grown in batch culture maintained in modified  
131 DIAT medium (Schlösser 1994). To avoid  $\text{HCO}_3^-$  limitation of photosynthesis, to reach the  
132 natural ionic strength of the lake ( $\text{HCO}_3^-$  range: 30-3000 mg L<sup>-1</sup>) and to attain the minimum  
133 conductivity threshold (3000  $\mu\text{S cm}^{-1}$ ) of saline conditions, 5.5 g  $\text{NaHCO}_3$  per liter was added  
134 to the culture medium. The medium was replaced by fresh medium in every 2nd-3rd week.  
135 The culture was maintained at 23 °C under photosynthetic active radiation (PAR) of 15  $\mu\text{mol}$

136  $\text{m}^{-2}\text{s}^{-1}$  and a 14:10 light:dark cycle was provided by cool white and daylight (1:1) fluorescent  
137 tubes.

### 138 *Laboratory experiments*

139 The study was carried out in a photosynthetron (Üveges et al. 2011). This incubation system  
140 consists of 9 cells with 9 different irradiances (0 - 8 - 35 - 70 - 110 - 200 - 400 - 800 - 1200  
141  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). The PAR was provided by daylight fluorescent tubes (Tungsram F74) at both  
142 sides of the photosynthetron and measured by a LI 1400 (LI-COR) equipped with a spherical  
143 ( $4\pi$ ) quantum micro sensor (US-SQS/L, Heinz Walz GmbH). The mirror inner walls  
144 multiplied and uniformed the irradiance. Permanent temperatures were kept constant by a  
145 circulating water bath (Neslab RTE-211).

146 *Nitzschia frustulum* culture was starved in sulphate and chloride-free modified DIAT  
147 medium for 2-3 weeks prior to the experiments for emptying cellular stocks of these ions and  
148 the applied soil extract was previously purified with  $\text{Ba}(\text{NO}_3)_2$  to eliminate its sulphate  
149 content via precipitation. After the starving, the culture was incubated in fresh modified DIAT  
150 medium and the experiments were started just after the culture reached the log phase of the  
151 growth curve, which was followed by optical density measurements. On the fifth day, the  
152 culture was homogenized and divided into Karlsruhe flasks. Three replicates were placed in  
153 each cells of the photosynthetron. The experiment was started at  $5^\circ\text{C}$  and after a one-hour  
154 pre-incubation in dark, the homogenous samples were further incubated for one or two hours  
155 depending on the density of the culture (Wetzel and Likens 2000). The dissolved oxygen  
156 concentration was measured at the beginning and at the end of the incubation period to  
157 determine photosynthetic activities (Wetzel and Likens 2000) using LDO sensor (HQ-20,  
158 Hach Lange) (Fig. 2). The chlorophyll-*a* was measured in acetone extracts (Wetzel and  
159 Likens 2000).

160 After the initial measurement, the culture was re-homogenized and re-divided into the flasks  
161 while the temperature was raised up to  $10^\circ\text{C}$  in the photosynthetron, and after the repeated  
162 pre-incubation, the dissolved oxygen and chlorophyll-*a* was measured again. This process was  
163 repeated six times at different ( $15 - 20 - 25 - 30 - 35 - 40^\circ\text{C}$ ) temperatures. After that, the  
164 diatom medium was replaced and the similar experimental design was applied for the two  
165 ionic gradients (Fig. 2). The gradients of the two anions ( $\text{Cl}^-$ ,  $\text{SO}_4^{2-}$ ) were established by  
166 adding  $\text{MgSO}_4$  and  $\text{MgCl}_2$  to the modified DIAT medium. Accordingly, 0 - 50 - 600 - 1200 -  
167 2400 - 3600 - 4800  $\text{mg L}^{-1} \text{SO}_4^{2-}$  and 0 - 36 - 437.5 - 875 - 1750 - 3500 - 5250  $\text{mg L}^{-1} \text{Cl}^-$   
168 concentrations were used by taking into consideration the mean and the full concentration

169 ranges of the anions measured in the soda pans. Concentrations of the anions were checked by  
170 titrimetric ( $\text{Cl}^-$ ) and spectrophotometric ( $\text{SO}_4^{2-}$ ) methods (APHA 1998). The surplus of the  
171 anions and the short incubation time ensured stable concentrations, furthermore, no  
172 precipitation was observed during the experiment. The pH was kept constant between 8-9 to  
173 provide sufficient carbon source for the photosynthesis. The conductivity of the medium was  
174 measured with multimeter (HQ40d Hach Lange). Table 2 summarizes the equivalences  
175 between the conductivity and the anion concentrations.

#### 176 *Data analyses*

177 Respiration, net and gross photosynthetic activities were calculated according to Wetzel  
178 and Likens (2000). For characterizing photosynthesis, the initial slope ( $\alpha$ ), the photoinhibition  
179 ( $\beta$ ) parameter and the photosynthetic rate ( $P_s$ ) were estimated by a formula described by  
180 (Platt, Gallegos, Harrison 1981) in GraFit program (Leatherbarrow 2009). The  $I_k$   
181 (photoadaptation parameter: the irradiance representing the onset of photosaturation) and  $P_m$   
182 (maximal photosynthetic rate) were scored. Spearman's rank correlation was applied to  
183 describe the relationships between the photoadaptation parameter ( $I_k$ ), the temperature and the  
184 ionic ( $\text{Cl}^-$ ,  $\text{SO}_4^{2-}$ ) concentrations using R Statistic program (Team 2010). Multiway ANOVA  
185 analyses were used to characterize the effects of the studied environmental factors on the  
186 photosynthetic activity.  $Q_{10}$  (temperature coefficient) model (Ahlgren 1987) was employed to  
187 characterize the response of the photosynthetic activity to different temperatures. To  
188 determine the optimum and tolerance ranges, the skewed normal distribution was used since it  
189 is widely applied in algal ecophysiological studies (Lehman et al. 1975; Dauta et al. 1990).  
190 The photosynthetic activity was normalized to unit chl-*a*.

## 191 **Results**

### 192 *P-I characteristics*

193 The mean values of photosynthetic activity were plotted as a function of the irradiances (P-I).  
194 Saturation curves were obtained in all cases and no photoinhibition ( $\beta$ ) was observed at any  
195 conductivities or temperatures (Fig. 3-4) within the applied light interval. The standard  
196 deviation of photosynthetic activity was less than 20 %. The gross photosynthetic activity  
197 measured in the sulphate and chloride-free medium were close to zero. The initial slope ( $\alpha$ ) of  
198 the P-I curve changed from 0.0010 to 0.0061 and from 0.0022 to 0.0233 along  $\text{Cl}^-$  and  $\text{SO}_4^{2-}$   
199 gradient respectively. The initial slope increased parallel with the conductivity (independently

200 of its ionic composition) up to 3600 mg L<sup>-1</sup> SO<sub>4</sub><sup>2-</sup> and 3500 mg L<sup>-1</sup> Cl<sup>-</sup> ion concentration. At  
 201 5250 mg L<sup>-1</sup> Cl<sup>-</sup> and 4800 mg L<sup>-1</sup> SO<sub>4</sub><sup>2-</sup> content there was a remarkable decline, which  
 202 approached 50% in most cases. This relationship was confirmed statistically and showed a  
 203 strong significant correlation between this parameter ( $\alpha$ ) and the ionic gradients ( $r \sim 0.9$ ,  
 204  $p > 0.01$ ).

205 The photoadaptation parameter ( $I_k$ ) ranged between 3 and 305  $\mu\text{mol m}^{-2} \text{s}^{-1}$  along both  
 206 ion gradients. Lower  $I_k$  values were estimated at the low temperatures and conductivities.  
 207 Based on the mean values, the photoadaptation parameter ( $I_k$ ) showed an increasing tendency  
 208 ( $r^2 = 0.97$ ) up to 30 °C in all media (Fig. 5). A similar relation was found between the  $I_k$  and the  
 209 conductivity gradients up to 3600 mg L<sup>-1</sup> SO<sub>4</sub><sup>2-</sup> ( $r^2 = 0.98$ ) and 3500 mg L<sup>-1</sup> ( $r^2 = 0.97$ ) Cl<sup>-</sup>  
 210 concentration (Fig. 6). Up to these values, the  $I_k$  increased exponentially along the SO<sub>4</sub><sup>2-</sup> and  
 211 linearly along the Cl<sup>-</sup> gradient. Above these concentrations a setback was measured. A strong  
 212 positive correlation ( $r^2 = 0.82$ ) was confirmed between the maximum photosynthetic rate and  
 213 the photoadaptation parameter.

214 Studying the SO<sub>4</sub><sup>2-</sup> gradient (Fig. 3), the gross photosynthetic rate (P) ranged between  
 215 0.02 and 3.48, while along Cl<sup>-</sup> gradient (Fig. 4) it varied between 0.01 and 1.52 mg C mg Chl-  
 216  $a^{-1} \text{h}^{-1}$ . The rate of photosynthesis in chloride medium did not exceed the 50% of the values  
 217 observed the sulphate-dominated medium in most cases. The photosynthetic activity of *N.*  
 218 *frustulum* was always lower in the diluted medium than in media characterized with high  
 219 conductivity. At the highest ion concentration a decline of the photosynthesis was measured at  
 220 each irradiance level and incubation temperature.

## 221 *Respiration*

222 The intensity of respiration increased both with temperature and conductivity along both  
 223 SO<sub>4</sub><sup>2-</sup> and Cl<sup>-</sup> gradients. Respiration values measured at 40 °C incubation temperature were  
 224 higher by at least 30 % than at 5 °C. Concerning ionic concentrations, similar differences  
 225 were observed: at both scales the relationship was strong between the two parameters as  
 226 approved by the correlation coefficient ( $0.5 < r^2 < 0.9$ ).

227 The photosynthesis:respiration ratio (P/R) was higher along SO<sub>4</sub><sup>2-</sup> than Cl<sup>-</sup> gradients; it  
 228 ranged from 0.54 to 11.61. Respiration consequently exceeded photosynthetic activity at the  
 229 lowest (5, 10 °C) and at the highest temperatures (35-40 °C). The P/R rate was close to or less  
 230 than 1.0 at the low ( $< 4600 \mu\text{S cm}^{-1}$ ) and high ( $> 9000 \mu\text{S cm}^{-1}$ ) conductivity levels. At  
 231 medium range of experimental conditions (15-35 °C and 4600-9000  $\mu\text{S cm}^{-1}$ ), the P/R ratio  
 232 was approximately 7 in the SO<sub>4</sub><sup>2-</sup>, and 4 in the Cl<sup>-</sup> media.



### 233 *P<sub>max</sub>-temperature-conductivity linkage*

234 The photosynthetic activity increased until 30-35°C independently from irradiance,  
 235 conductivity or ionic composition. At the low temperatures (5-10°C), lower photosynthetic  
 236 rates (<0.3 mgC mgChl-*a*<sup>-1</sup> h<sup>-1</sup>) were measured than at higher incubation temperatures.

237 The estimated Q<sub>10</sub> values varied between 0.74 and 2.08 along the SO<sub>4</sub><sup>2-</sup>, and between  
 238 1.17 and 2.20 along the Cl<sup>-</sup> gradients. The Q<sub>10</sub> was less than 1 only at very low irradiance (8  
 239 μmol m<sup>-2</sup> s<sup>-1</sup>) levels in the sulphate-dominated medium.. At the medium irradiance levels (30-  
 240 200 μmol m<sup>-2</sup> s<sup>-1</sup>) the average Q<sub>10</sub> was 1.87±0.18 (SO<sub>4</sub><sup>2-</sup> gradient) and 1.63±0.21 (Cl<sup>-</sup> gradient)  
 241 (Fig. 7). At higher irradiances, the Q<sub>10</sub> values exceeded 2, which is a strong correlation  
 242 between the temperature and the photosynthesis.

243 The maximal photosynthetic rate (P<sub>max</sub>) reached 1.57 mgC mgChl-*a*<sup>-1</sup> h<sup>-1</sup> along the  
 244 chloride, 3.62 mgC mgChl-*a*<sup>-1</sup> h<sup>-1</sup> along the SO<sub>4</sub><sup>2-</sup> gradient. The lowest values (average  
 245 P<sub>max</sub>=0.24 and 0.07) were measured in the most diluted media (50 mg L<sup>-1</sup> SO<sub>4</sub><sup>2-</sup> and 36 mg L<sup>-1</sup>  
 246 Cl<sup>-</sup> respectively). There were positive correlations between the maximal photosynthesis and  
 247 the ion gradients up to 3600 mg L<sup>-1</sup> SO<sub>4</sub><sup>2-</sup> and 3500 mg L<sup>-1</sup> Cl<sup>-</sup> content, beyond which reduced  
 248 values were measured again. This relation was independent of the temperature (Fig. 8). The  
 249 photosynthetic activity reached its maximum determined by Gauss fitting at 3253±106 mg L<sup>-1</sup>  
 250 chloride (8904±148 μS cm<sup>-1</sup>) and 3332±120 mg L<sup>-1</sup> SO<sub>4</sub><sup>2-</sup> concentration (8519±106 μS cm<sup>-1</sup>).

251 In regard of the temperature, a similar tendency was recognized. The photosynthetic  
 252 activity was augmented parallel with the increasing temperature up to 30 °C. At higher  
 253 temperatures, a decrease of the photosynthesis was observed at each conductivity levels. The  
 254 maximum photosynthesis-temperature curve illustrated on Fig. 9 had a peak at 28.5 ± 0.5 °C  
 255 that appeared to be independent of the ion content of the media and the irradiance.

### 256 **Discussion**

257 In 2006 and 2008, approximately 100 diatom samples were collected for a compositional  
 258 survey from altogether 31 Hungarian and Austrian shallow, alkaline, saline lakes (Stenger-  
 259 Kovács et al. 2014). According to the redundancy analyses (RDA) *Nitzschia frustulum* was  
 260 one of the dominant species in the lakes of Fertő-Hanság region, where the SO<sub>4</sub><sup>2-</sup> dominance  
 261 is characteristic, while the Cl<sup>-</sup> concentration is low (Boros et al. 2014; Stenger-Kovács et al.  
 262 2014). Due to the climate change, increasing conductivity, Cl<sup>-</sup> and SO<sub>4</sub><sup>2-</sup> concentrations as  
 263 well as higher temperature records and changing light depending on the water level can be  
 264 predicted in saline, shallow lakes.

265 *Ion preference*

266 *N. frustulum* prefers more  $\text{SO}_4^{2-}$  (max. photosynthesis was  $3.62 \text{ mgC mgChl-}a^{-1} \text{ h}^{-1}$ ) than  $\text{Cl}^-$   
267 (max. photosynthesis was  $1.52 \text{ mgC mgChl-}a^{-1} \text{ h}^{-1}$ ) (Fig. 8) supporting the results of the  
268 ecological analyses of diatom assemblages in shallow saline lakes (Stenger-Kovács et al.  
269 2014). The P/R ratio also supported that the population kept in  $\text{SO}_4^{2-}$  dominated medium  
270 maintained healthier condition, than that in  $\text{Cl}^-$  dominated medium ( $p < 0.05$ ). The difference  
271 can be explained with the roles of these two major anions. The biochemical role of sulphur is  
272 more important and diversified than that of chloride. Sulphur is an important constituent of  
273 proteins (cysteine and methionine), coenzymes and vitamins (thiamine and biotin) which  
274 facilitate uptake of the divalent ions, while the coenzymes have important role of the  
275 respiration and fatty acid metabolism. Furthermore, sulfur has a main role in the electron  
276 transfer reaction of photosynthesis (ferredoxin) and in the nitrogen fixation (Hopkins and  
277 Hüner 2004b). However,  $\text{SO}_4^{2-}$  is a competitive inhibitor of molybdenate uptake (Cole et al.  
278 1986) which has an important role of the  $\text{NO}_3^-$  uptake by being a component of enzymes  
279 involved in its reduction. Based on this process, the inhibition of the photosynthetic activity of  
280 *N. frustulum* was also expected under higher  $\text{SO}_4^{2-}$  content similarly as supposed by Cole et  
281 al. (1986) for phytoplankton communities. In contrast,  $\text{Cl}^-$  has two key roles, one is the  
282 photosynthetic oxygen evolution and the other is the maintenance of charge balance across  
283 cellular membranes.  $\text{Cl}^-$  is a counterion to several diffusible cations and, due to its mobility,  
284 can maintain electrical neutrality across cellular membranes. It is very important in habitats,  
285 where the salinity is high. In the Hungarian small saline lakes,  $\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{Mg}^{2+}$  and  $\text{Ca}^{2+}$  are the  
286 main cations that need to be counterbalanced by  $\text{Cl}^-$ . In summary, the  $\text{Cl}^-$  is one of the principal  
287 osmotically active solutes in the vacuole (Hopkins and Hüner 2004b), however, at high  
288 amounts of this ion, it becomes toxic element (Hopkins and Hüner 2004b). Survival of  
289 organisms and their photosynthetic activity under salinity stress implies effective  
290 osmoregulation (Bauld 1981). However, salt stress increases the accumulation of toxic  $\text{Cl}^-$  in  
291 chloroplasts causing decrease in photosynthetic electron transport activities (Boyer 1976;  
292 Kirst 1990). In the present study, concentrations higher than  $3300 \text{ mg L}^{-1}$  appeared to be  
293 toxic. Blinn (1993) reported that *N. frustulum* is indicative to high conductivities, since this  
294 species occurred between  $1500\text{-}30000 \text{ } \mu\text{S cm}^{-1}$ . The species has high SCI (specific  
295 conductance index) and IonI (ion index) values (these indices provide a relative numeric scale  
296 to evaluate various diatom species along these environmental factors) which means close

297 positive association between the abundance of the diatom taxa and the high  $\text{SO}_4^{2-}$ ,  $\text{Na}^+$  and  $\text{Cl}^-$   
298 ions (Blinn 1993).

### 299 *The optimal ion concentrations and conductivity*

300 The maximum photosynthetic rate was detected at  $3253 \pm 106 \text{ mg L}^{-1} \text{ Cl}^-$  ( $8904 \pm 48 \text{ } \mu\text{S cm}^{-1}$ )  
301 and  $3332 \pm 120 \text{ mg L}^{-1} \text{ SO}_4^{2-}$  concentration ( $8519 \pm 106 \text{ } \mu\text{S cm}^{-1}$ ) independently from the  
302 temperature (Fig. 8). The difference in the conductivity ( $\sim 400 \text{ } \mu\text{S cm}^{-1}$ ) could be explained  
303 with the differences in the DIAT medium: in the  $\text{Cl}^-$  dominated medium-low  $\text{SO}_4^{2-}$   
304 concentration was used to reach the minimum limit for the sufficient biochemical function,  
305 which lead to increased conductivity level. The above values can be considered as optima of  
306 the species, which is, nevertheless, described cosmopolitan (Krammer and Lange-Bertalot  
307 1997). At salinity levels above  $8900 \text{ } \mu\text{S cm}^{-1}$ , inhibition of photosynthetic activity was  
308 observed in our study. Available floristic studies report on dominance of *Nitzschia frustulum*  
309 at low salinities ( $3\text{-}4000 \text{ } \mu\text{S cm}^{-1}$ ) (Veres, Pienitz, Smol 1995) and in mesohaline conditions  
310 above  $3000 \text{ mg L}^{-1} \text{ Cl}^-$  ( Ziemann 1971, 1972; Busse et al. 1999; Ziemann et al. 2001) , and  
311 there is no information about occurrence along a  $\text{SO}_4^{2-}$  gradient. An interesting strategy of *N.*  
312 *frustulum* was demonstrated by Trobajo et al. (2004) that may contribute to its tolerance of  
313 higher conductivity levels. The species can alter its length-width ratio parallel with the  
314 alteration of the salinity range. Similarly, longer frustules were found at higher conductivity  
315 levels in another study (Busse et al. 1999). The variation of the frustules shape, cell size or  
316 colony size in the view of the salinity stress is not unique: it is a well-known strategy among  
317 the unicellar algae (Kirk 1994). However, these papers are based on floristic surveys and  
318 monitoring investigations, while the ecophysiological experiments have been missing.

319 In response to osmotic stress, *N. frustulum* may have strategy by synthesizing a co-  
320 soluted, osmoregulation metabolites to avoid the damage (Sudhir and Murthy 2004), which  
321 was not investigated in the present study. According to our study, *N. frustulum* can tolerate  
322 the gradually increasing conductivity thus gaining ecological benefit in hyposaline waters.

### 323 *The productivity of N. frustulum*

324 Maximal biomass specific photosynthetic rate of phytoplankton in Australian, African and  
325 American saline lakes (Hammer 1981) ranged between  $1.17$  and  $38.88 \text{ mgC mgChl-}a^{-1} \text{ h}^{-1}$   
326 with an average value of  $9.42 \text{ mgC mgChl-}a^{-1} \text{ h}^{-1}$ . Sarthou et al. (2005) highlighted the  
327 considerable photosynthetic activity and growth values of diatoms among the algae, with their  
328 maximal specific rate of photosynthesis ( $2.6 \pm 1.0 \text{ mgC mgChl-}a^{-1} \text{ h}^{-1}$ ). According to Hammer  
329 (1981), the most productive lakes can be characterized with high pH (9-10.5), SRP (soluble

330 reactive phosphate) concentration and alkalinity in contrast to very low nitrate content. These  
331 features are typical for the lakes in Fertő-Hanság region, where the photosynthetic activity of  
332 one of the most dominant species, *Nitzschia frustulum* ( $\sim 4 \text{ mgC mgChl-}a^{-1} \text{ h}^{-1}$ ) is not far from  
333 the productivity of the phytoplankton measured previously by Hammer (1981).

#### 334 *Light preference*

335 Sediment surfaces of the shallow lakes can be excellent habitats for the epipellic algal  
336 assemblages since adequate light is available (Hill 1996). The light compensation point of *N.*  
337 *frustulum* was  $\sim 20 \mu\text{mol m}^{-2}\text{s}^{-1}$  independently from conductivity, anion concentration or  
338 temperature. Our results may provide another possible explanation why this species is  
339 abundant only in the Fertő-Hanság region. In this region, the suitable light intensity always  
340 persists, contrary to the lakes situated in the Danube-Tisza Interfluve, where low light levels  
341 ( $< 20 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) can be measured during most of the time (V.-Balogh et al. 2009). The  
342 photosynthetic rate of *Nitzschia frustulum* becomes light-saturated already at medium light  
343 intensities ( $< 250 \mu\text{mol m}^{-2}\text{s}^{-1}$ ). Based on the photoadaptation parameter ( $I_k$ ), with the  
344 increasing temperature and conductivity the species needs higher light intensity to maximize  
345 its photosynthetic processes similar to other algae like *Chlorella*, *Synechocystis*, *Fragilaria* as  
346 well as *Staurastrum* sp. (Dauta et al. 1990). This condition (as the required medium  
347 irradiance) is sufficed in the field, since as summer progresses, salt contents in the soda pans  
348 are concentrating, their water levels lower and their transparency increases. Similar to *N.*  
349 *frustulum*, *Pseudo-Nitzschia multiseries* is also acclimated to medium irradiances ( $< 250 \mu\text{mol}$   
350  $\text{m}^{-2}\text{s}^{-1}$ ) with a maximum photosynthesis of only  $1.16 \text{ mC mgChl-}a^{-1} \text{ h}^{-1}$  measured at  $10 \text{ }^\circ\text{C}$   
351 (Pan et al. 1996; Sarthou et al. 2005). Based on the medium  $I_k$  (range from 5 to  $305 \mu\text{mol m}^{-2}$   
352  $\text{s}^{-1}$ , Fig. 5-6) of *Nitzschia frustulum* can be good light competitor similar to many  
353 cyanobacteria ( $10\text{-}231 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) and most green algae ( $85\text{-}510 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) (Reynolds  
354 1988; Padisák 2004). Similarly, *Anabaena minderi* and *A. torques* as the members of the  
355 phytobenthos exhibited the highest growth rates at low irradiances ( $75 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) indicating  
356 their adaptation to low light conditions (de Tezanos Pinto and Litchman 2010). However,  
357 acclimation to low irradiances is often combined with photoinhibition at high irradiances  
358 (Belay and Fogg 1978). A benthic community growing in shallow water is exposed to high  
359 irradiance, which cause photooxidative decay of chlorophyll pigments in presence of oxygen  
360 (Kirk 1994). Despite these environmental conditions can prevail in the Fertő-Hanság region  
361 ( $30\text{-}2300 \mu\text{mol m}^{-2}\text{s}^{-1}$  irradiance and  $1.5\text{-}18 \text{ mg L}^{-1}$  dissolved oxygen was measured),  
362 photoinhibition was not observed in our study, which can contribute to the success of the

363 species. Based on several studies carried out on sand flat and planktonic diatoms,  
364 photosynthesis is usually inhibited at moderate light intensities around 600-1200  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ,  
365 or at higher levels ( $>1200 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) (Taylor 1964; Whitney and Darley 1983).

366 There are different strategies of this species to avoid the photooxidative damage.  
367 Physiologically, *Nitzschia frustulum* may synthesize more secondary photoprotective  
368 pigments, like carotenoids (Krumbein et al. 1977) in the form of fukoxantin. The function of  
369 these secondary pigments is to cover the chlorophylls protecting them from the direct light  
370 (Kirk 1994). The life form of the species can serve another way to avoid this damage. The  
371 genus *Nitzschia* belongs to the motile guild (they do not attach to the substrates), and these  
372 species are able to change their position in the benthic layer to find the most adequate habitats  
373 (Passy 2007). Thus, in seasons with high irradiation and low water levels, motility enables  
374 motile species to find microrefuges with lower light. However, in some seasons low solar  
375 radiation and high turbidity seriously reduce underwater light availability. Besides the good  
376 light harvesting efficiency (net photosynthesis occur around 20  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ), the life form of  
377 the species is also helpful in these environments. Additionally, taxa which are adapted to low-  
378 light conditions, may exhibit diurnal vertical movements thus regulating their position in the  
379 benthos (Hill 1996). Therefore, phototaxis may play a major role in their primary production  
380 (Kemp et al. 2000) under reduced light conditions. The high turbidity of shallow, saline lakes  
381 is originating from the high inorganic seston content (V.-Balogh et al. 2009) restricts light  
382 intensity, but by altering carotenoid:chlorophyll ratio (Jorgensen 1979) or changing location,  
383 *N. frustulum* can tolerate or survive the unfavorable environmental conditions, which  
384 confirms the flexibility of the *Nitzschia* species under stressed conditions. This flexibility was  
385 confirmed by the  $Q_{10}$  values of the species, as it raised exponentially which indicates  
386 increasing enzymatic reactions. The  $Q_{10}$  values varied between (0.74) 1.17 and 2.20. It  
387 reached 1.93 at medium light intensity (110  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ). According to (Reynolds 1988),  
388 species with 1.9-3.4 of  $Q_{10}$  are R-strategists with high metabolic activities and rapid growth  
389 rates.

#### 390 *Temperature preference*

391 For *N. frustulum*, the optimal temperature of the photosynthesis was found at 27-28 °C (Fig.  
392 9). Its tolerance ( $2\sigma$  of the Gauss curve) ranges between 20 and 35 °C. The observed normal  
393 distribution is characteristic for temperate diatoms rather than for the polar populations where  
394 the optimum curve is less symmetric (Fiala and Oriol 1990). Other *Nitzschia* species like *N.*  
395 *closterium* reached its maximal photosynthesis at about 27 °C, while *N. palea* found in soil or

396 in small water bodies was able to survive high temperatures (35 °C) (Barker 1935).  
397 Sensitivity of *N. frustulum* to cold water temperatures is demonstrated by parallel decrease in  
398 a photosynthetic activity. Low temperatures may cause irreversible changes, for example in  
399 membrane fluidity (Falkowski and Raven 1997). On the other side of the optimum curve (35  
400 °C in the case of *N. frustulum*) photosynthetic efficiency is reduced because of denaturation  
401 of enzymes at high temperatures (Hopkins and Hüner 2004a). The photosystem II and the  
402 oxygen evolving complex inactivate and the fluidity of the thylakoid membranes (Falkowski  
403 and Raven 1997; Hopkins and Hüner 2004a). Salinity, light and temperature are important  
404 environmental variables influencing species abundance via affecting the photosynthetic  
405 process (Oppenheim 1991; Underwood 1994; Underwood et al. 1998). Based on the ANOVA  
406 analyses the main photosynthetic parameters of *N. frustulum* are principally determined by  
407 temperature rather than conductivity and light, contrary to *Pseudo-Nitzschia granii* (El-  
408 Sabaawi and Harrison 2006).

409  
410 In summary, *Nitzschia frustulum* prefers high temperature (28.5 °C) and conductivity (8599  
411  $\mu\text{S cm}^{-1}$ ) values, which are typical characteristics of the shallow soda pans. *N. frustulum*  
412 showed more intensive photosynthetic activity in  $\text{HCO}_3^-$ - $\text{SO}_4^{2-}$ , than in  $\text{HCO}_3^-$ - $\text{Cl}^-$  dominated  
413 media. This ion preference and the medium irradiance demand of the species may explain its  
414 dominance in the Fertő-Hanság region. The species is tolerant to a broad range of salinities,  
415 which can be observed due to the extreme weather events (eg. Droughts or sudden and heavy  
416 rainfalls). It can occupy a broad niche (Reynolds 1988; Reynolds and Kinne 1997), which  
417 represents an ecological advantage (Litchman and Klausmeier 2008) against other diatom  
418 species. Nevertheless, its photosynthetic transport chain will slow down resulting in a  
419 decrease in the photosynthetic activity under increasing, sometimes extreme temperatures  
420 (observed in the field (Vörös and Boros 2010)) and predicted by the climate change models.

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#### 427 **Legends**

- 428 **Table 1.** The chemical and physical features measured previously in Borsodi-dűlő
- 429 **Table 2.** The conductivity of the mediums used during the experiment
- 430 **Fig. 1.** Light- (1-4) and electronmicroscopic (5-6) photos about *Nitzschia frustulum* culture
- 431 (scales: 10  $\mu\text{m}$ )
- 432 **Fig. 2.** A schematic flow chart of the laboratory experiments (3R: three replicates; PA: the
- 433 measurements of the photosynthetic activity; LI: irradiance; reh.: rehomogenization; w: week;
- 434 d: day; h: hour)
- 435 **Fig. 3.** The mean, gross photosynthesis-irradiance (P-I) curves of *Nitzschia frustulum*.
- 436 measured along sulphate gradients at different incubation temperatures
- 437 **Fig. 4.** The mean, gross photosynthesis-irradiance (P-I) curves of *Nitzschia frustulum*
- 438 measured along chloride gradients at different incubation temperatures
- 439 **Fig. 5.** The variation of the photoadaptation parameters ( $I_k$ ) observed at the different
- 440 incubation temperatures along sulphate (A) and chloride (B) gradient
- 441 **Fig. 6.** The variation of the photoadaptation parameters ( $I_k$ ) observed along the sulphate-
- 442 dominated (A) and chloride-dominated (B) conductivity gradients
- 443 **Fig. 7.** The mean Q10 values of the photosynthetic activity of *Nitzschia* sp measured at nine
- 444 irradiance levels
- 445 **Fig. 8.** The maximum photosynthetic activity of *Nitzschia frustulum* measured in the different
- 446 ion-concentrations mediums and incubation temperatures based on the mean values of gross
- 447 photosynthesis-irradiance (P-I) curves
- 448 **Fig. 9.** The maximum photosynthetic rate-temperature curves of the *Nitzschia frustulum*
- 449 measured along the sulphate (A) and chloride ion (B) gradients based on the mean values of
- 450 gross photosynthesis-irradiance (P-I) curves

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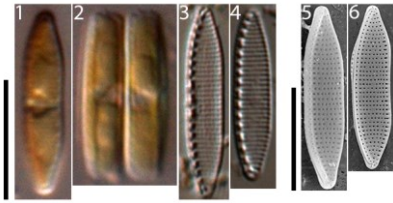
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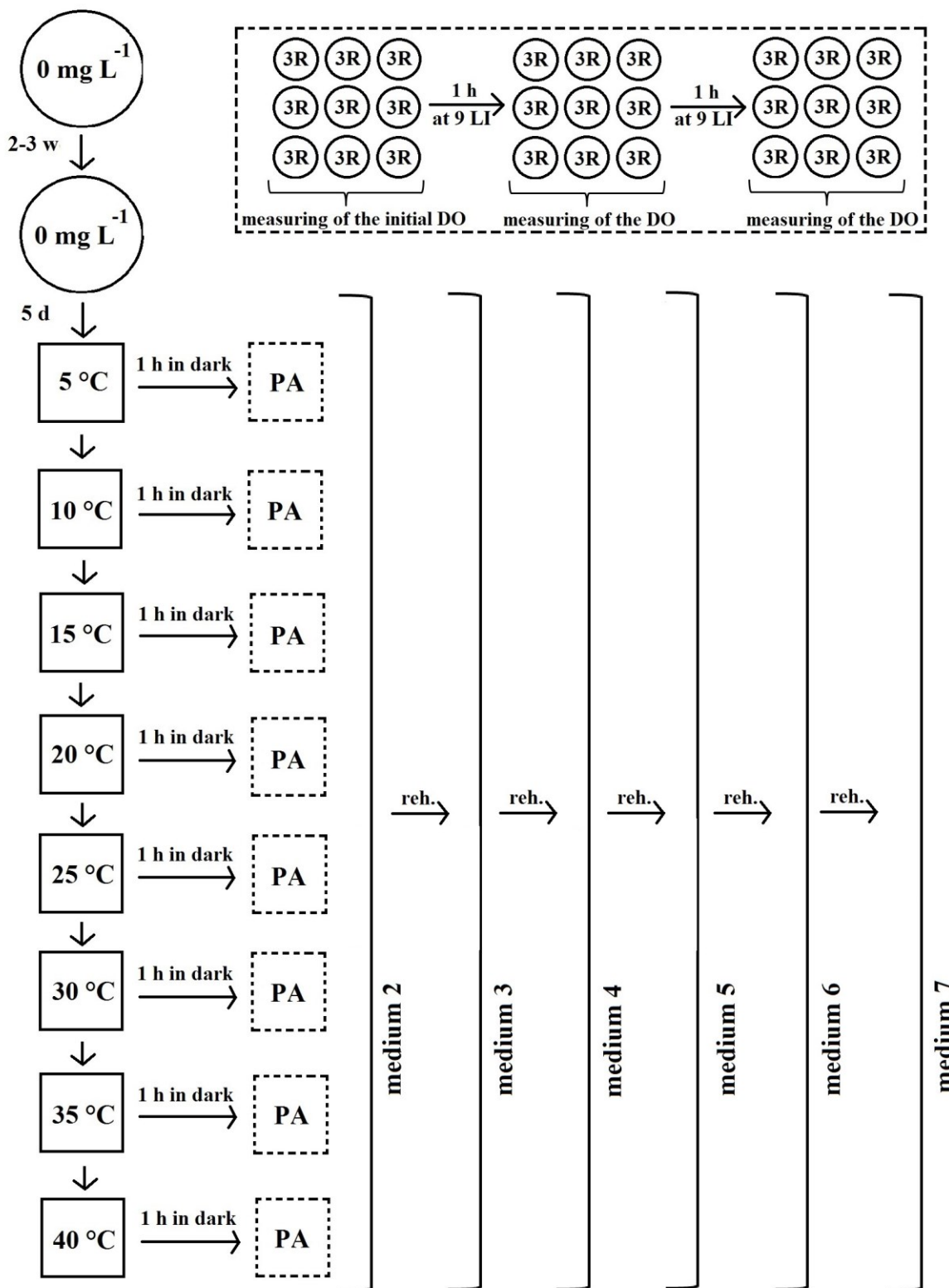
728 Fig. 1



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730

731 Fig. 2

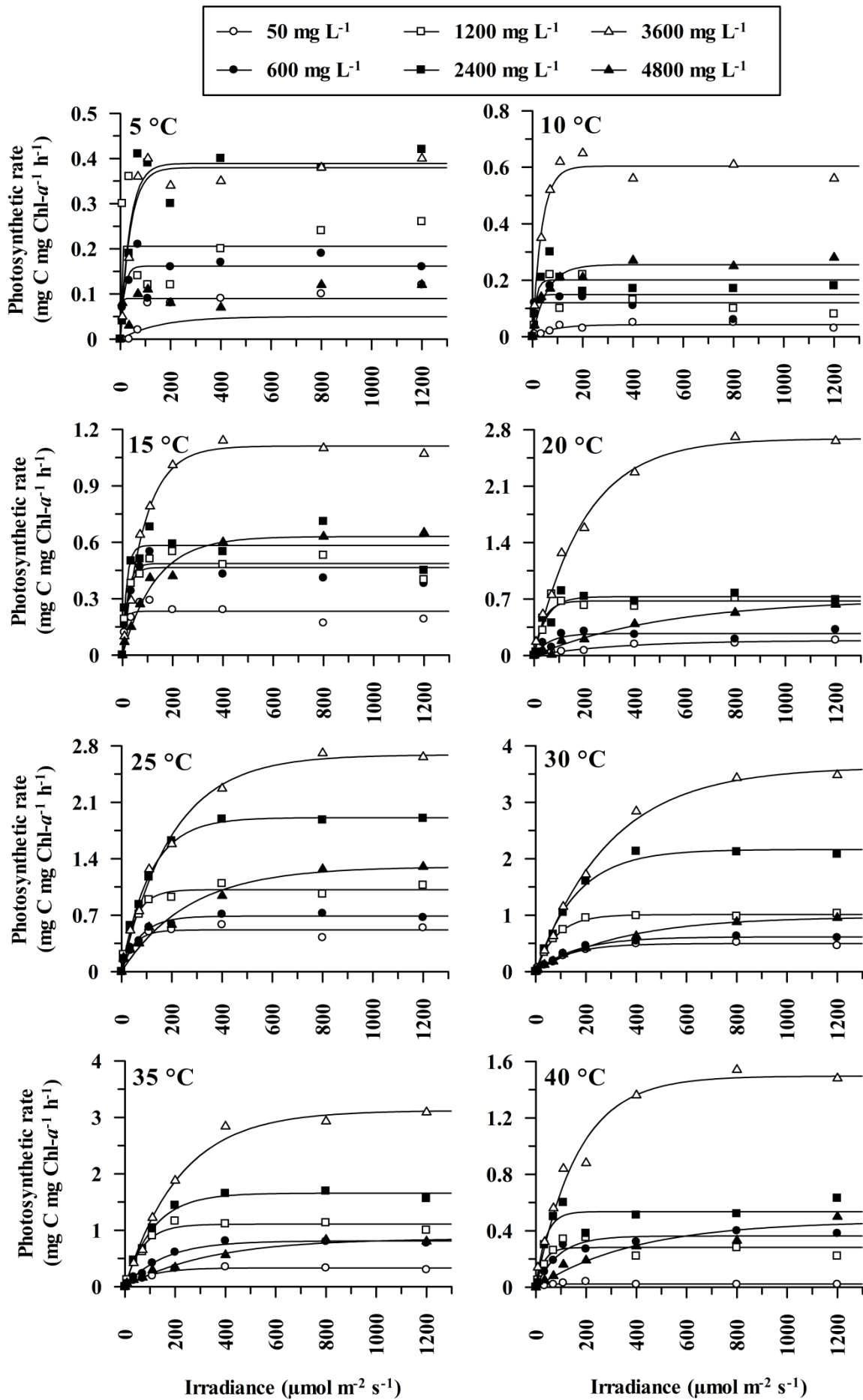


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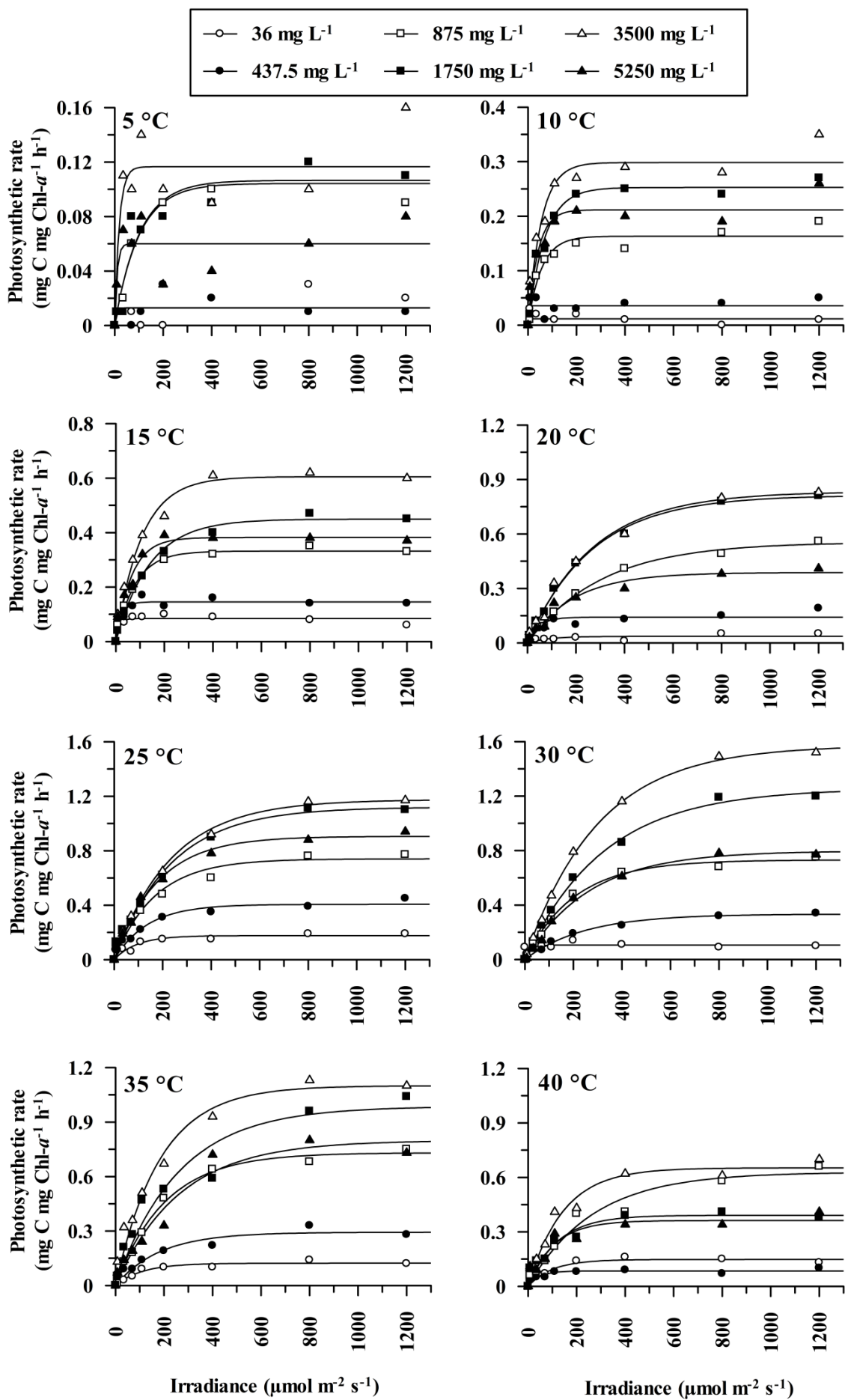
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734 Fig. 3

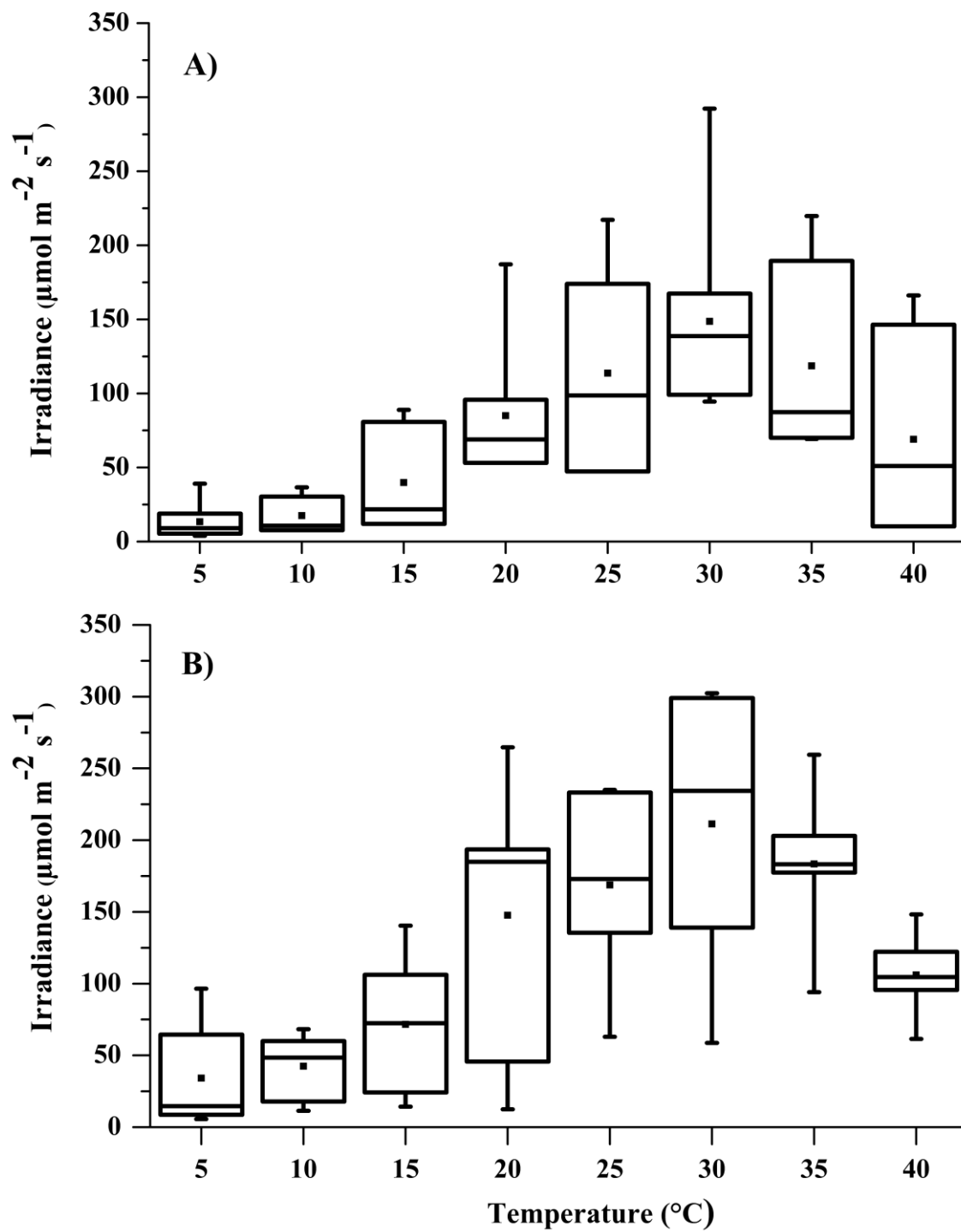




736 Fig. 4



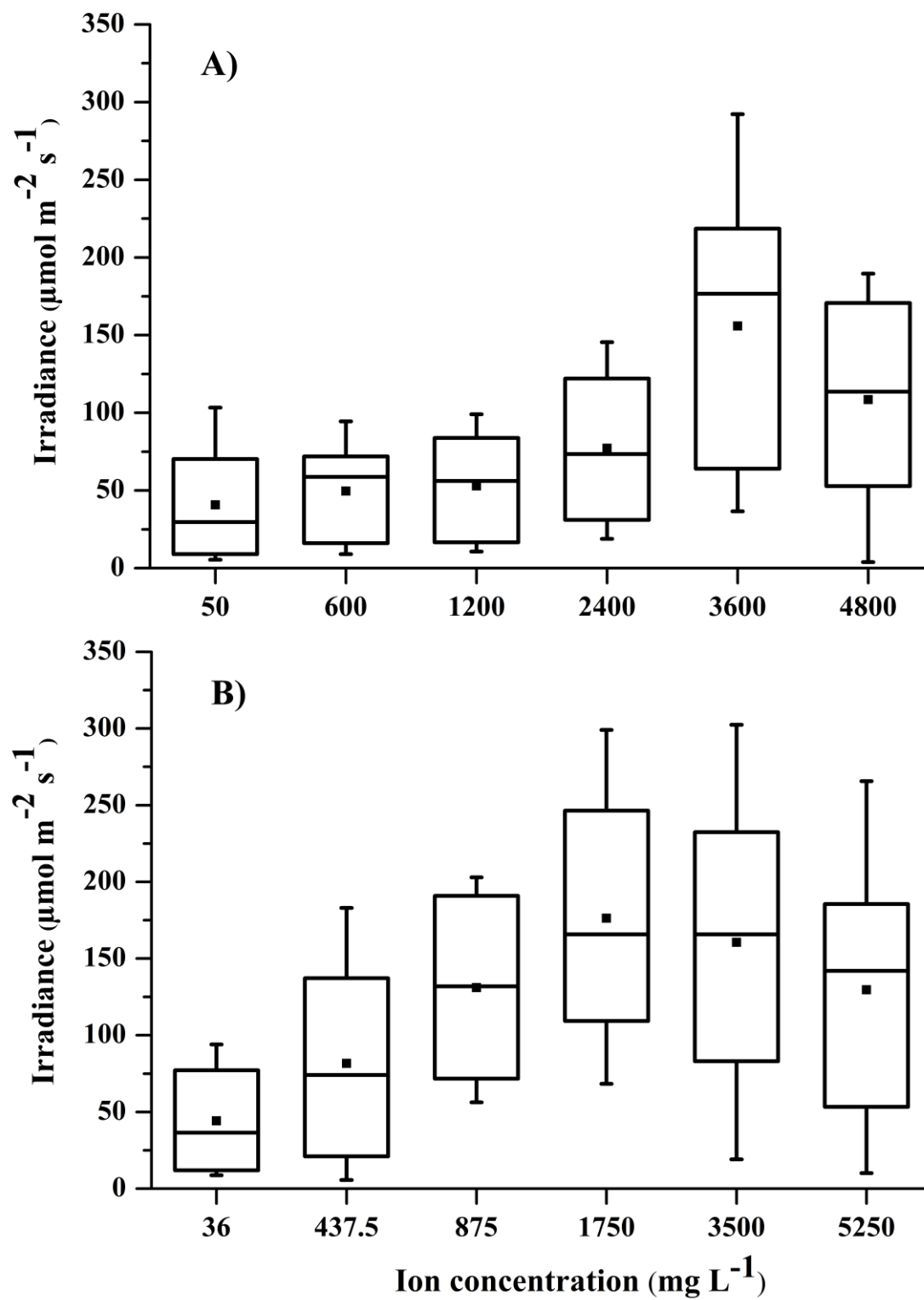
738 Fig. 5



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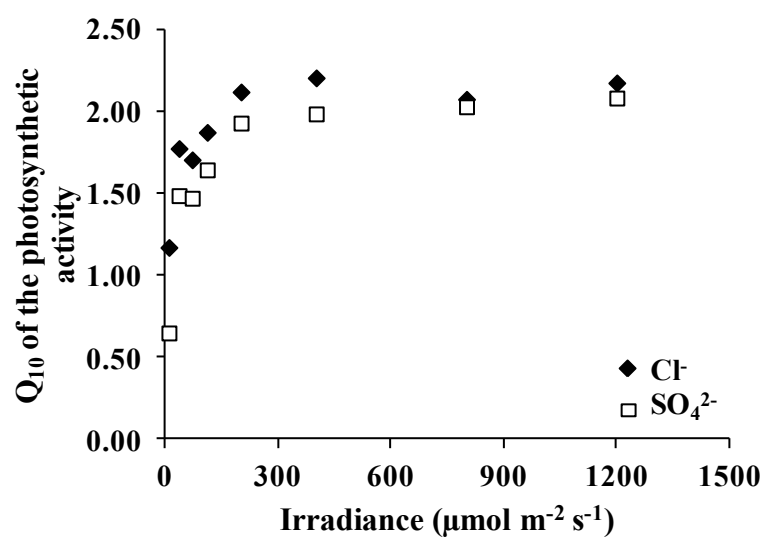
741 Fig. 6



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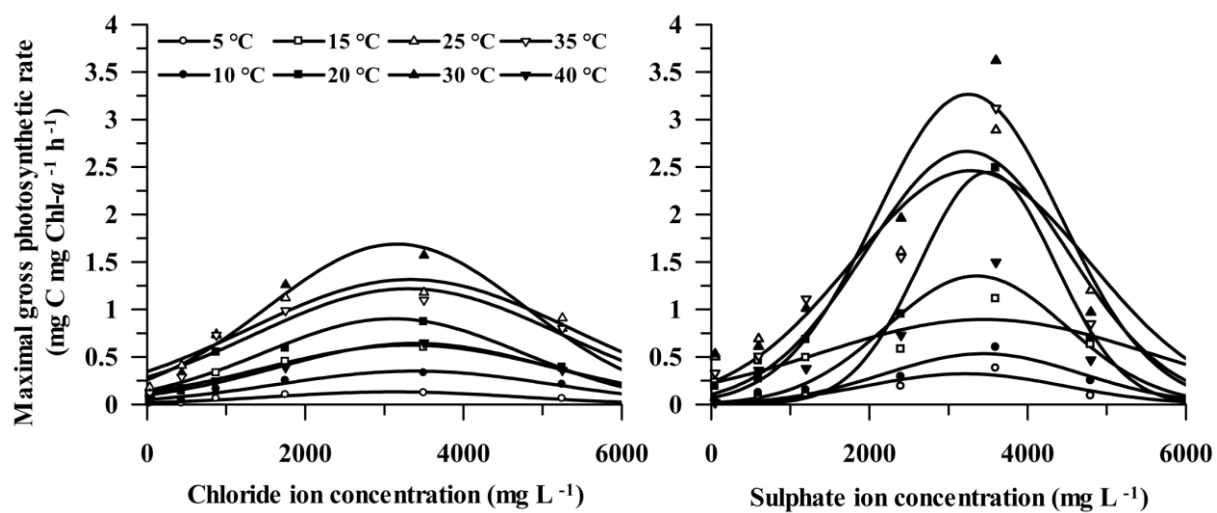
744 Fig. 7



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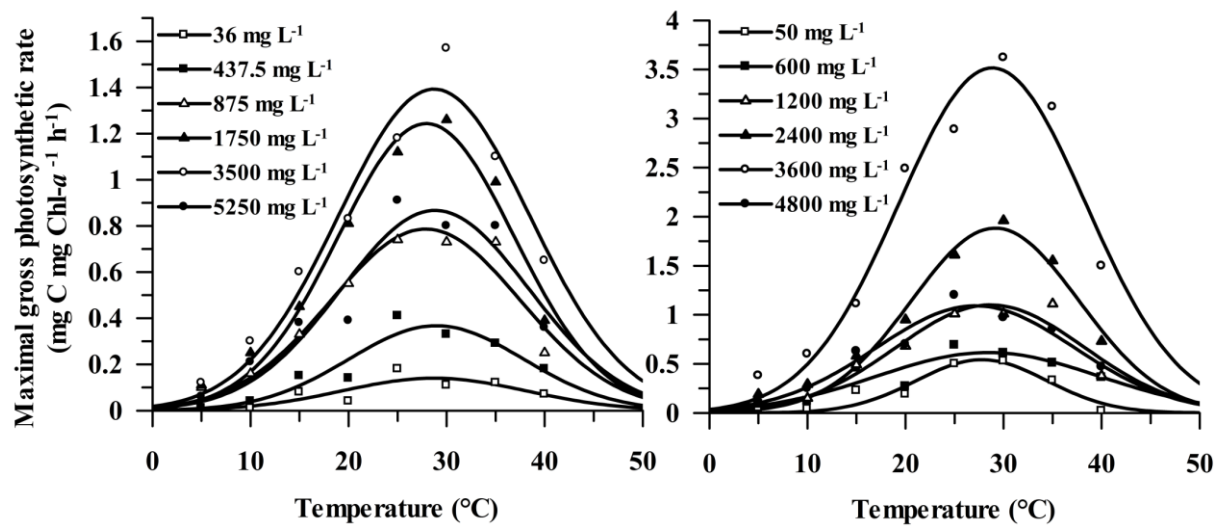
747 Fig. 8



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750 Fig. 9



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753 Table 1

	Unit	Sample number (n)	Min.	Max.	Mean (m)	Standard deviation (sd)
<b>Dissolved oxygen (DO)</b>	<b>mg L<sup>-1</sup></b>	22	1.5	18.0	9.9	3.6
<b>Oxygen saturation</b>	<b>%</b>	22	18.1	197.2	93.7	35.6
<b>pH</b>		21	8.1	9.6	8.9	0.4
<b>Conductivity</b>	<b>μS cm<sup>-1</sup></b>	22	1061	8150	2715	1757
<b>Temperature</b>	<b>°C</b>	22	1.7	25.0	13.2	7.8
<b>Turbidity</b>	<b>FNU</b>	9	35.2	1321.0	407.7	511.4
<b>Light intensity</b>	<b>μmol m<sup>-2</sup> s<sup>-1</sup></b>	16	30	2300	591	681
<b>COD</b>	<b>O<sub>2</sub> mg L<sup>-1</sup></b>	15	9.7	59.5	31.1	14.4
<b>Cl<sup>-</sup></b>	<b>mg L<sup>-1</sup></b>	15	20.1	729.5	220.2	163.3
<b>HCO<sub>3</sub><sup>-</sup></b>	<b>mg L<sup>-1</sup></b>	15	42.7	1446.3	586.9	331.6
<b>CO<sub>3</sub><sup>2-</sup></b>	<b>mg L<sup>-1</sup></b>	15	0.0	255.0	85.4	86.1
<b>SO<sub>4</sub><sup>2-</sup></b>	<b>mg L<sup>-1</sup></b>	15	32.1	1665.0	269.0	404.0
<b>NO<sub>2</sub><sup>-</sup></b>	<b>μg L<sup>-1</sup></b>	15	2.1	71.8	12.0	18.0
<b>NO<sub>3</sub><sup>-</sup></b>	<b>mg L<sup>-1</sup></b>	13	0.0	1.6	0.5	0.4
<b>NH<sub>4</sub><sup>+</sup></b>	<b>mg L<sup>-1</sup></b>	13	0.0	0.3	0.1	0.1
<b>SiO<sub>2</sub></b>	<b>mg L<sup>-1</sup></b>	15	0.5	21.4	6.2	5.7
<b>PO<sub>4</sub><sup>3-</sup></b>	<b>μg L<sup>-1</sup></b>	15	5.9	351.8	149.2	108.5
<b>TP</b>	<b>μg L<sup>-1</sup></b>	14	147.6	5120.0	907.6	1272.9
<b>Colour</b>	<b>mg Pt<sup>-1</sup></b>	12	8.2	129.8	32.1	33.3

754

755

756 Table 2

<b>Cl<sup>-</sup></b> <b>(mg L<sup>-1</sup>)</b>	<b>Conductivity</b> <b>(μS cm<sup>-1</sup>)</b>	<b>SO<sub>4</sub><sup>2-</sup></b> <b>(mg L<sup>-1</sup>)</b>	<b>Conductivity</b> <b>(μS cm<sup>-1</sup>)</b>
36	4100	50	4300
437.5	4550	600	4660
875	5740	1200	6000
1750	6940	2400	7430
3500	9370	3600	8770
5250	11670	4800	10010

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