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## Laboratory growth capacity of an invasive cyanobacterium (*Microcystis aeruginosa*) on organic substrates from surface waters of permafrost peatlands

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1      **Laboratory growth capacity of an invasive cyanobacterium (*Microcystis***  
2      ***aeruginosa*) on organic substrates from surface waters of permafrost**  
3      **peatlands**

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14  
15     **Key words:** thermokarst lake, moss, lichen, growth, proliferation, laboratory experiment

16     **Target journals:** *Environmental Science: Processes and Impacts*

17  
18     **Highlights:**

- 19     ● *M. aeruginosa* proliferated on aqueous leachates of lichen, moss and peat
- 20     ● pH rise by 2 units due to *M. aeruginosa* growth on natural organic substrates
- 21     ● Sizable DOC uptake by proliferating cyanobacteria
- 22     ● Increase in SUVA<sub>254</sub> due to uptake of optically transparent DOC
- 23     ● Summer-time bloom of invasive cyanobacteria can offset lake CO<sub>2</sub> evasion

## 26 **Abstract**

27        Within a global warming trend, invasive cyanobacteria, abundant in tropical and temperate  
28 regions, can migrate northward and colonize thermokarst lakes in permafrost-affected  
29 territories. Towards a better understanding of the cyanobacterial proliferation mechanism in  
30 those lakes, we performed laboratory growth of typical invasive cyanobacteria, *Microcystis*  
31 *aeruginosa*, onto various organic-rich solutions representative of permafrost peatlands.  
32 Aqueous leachates of lichen, moss and peat were the most favorable substrates for massive  
33 growth. The growth in the presence of all organic substrates produced a rise in solution pH by  
34 two units and a sizable (30-50%) decrease in the concentration of dissolved organic carbon.  
35 The observed increase of dissolved organic carbon aromaticity degree likely reflected  
36 preferential cyanobacterial uptake of aliphatic, optically transparent organic substances.  
37 Cyanobacterial growth over a bloom period can create a carbon sink (uptake of 2.5 and 8.3 g  
38 C-CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) that can offset the net heterotrophic status of thermokarst lakes in the permafrost  
39 peatlands, thus switching the lake status from C source to C sink. Therefore, predictions of the  
40 future carbon exchanges with the atmosphere in surface waters of permafrost peatlands require  
41 explicit accounting for the possibility of invasive cyanobacterial growth.

42

## 43 **1. Introduction**

44        On-going warming of the Arctic and subarctic surface waters is accompanied by more  
45 frequent summer heatwaves inducing an increase in lakes water temperature up to 25-30 °C<sup>1,2</sup>.  
46 In this regard, thermokarst lakes, formed during massive and abrupt peat thaw in currently  
47 frozen permafrost peatland, are especially interesting as they cover a sizable portion of land  
48 surface in the Arctic and subarctic zone<sup>3-6</sup>. Due to their generally heterotrophic status, the  
49 dominance of dissolved organic matter (DOM) and sediment respiration on primary production,

50 these lakes emit a sizable amount of CO<sub>2</sub> and CH<sub>4</sub> in the atmosphere, thus contributing to  
51 positive feedback to climate warming at high latitudes <sup>7-9</sup>.

52 A growing concern for all freshwater environments of the world is the development of  
53 invasive cyanobacterial blooms primarily due to climate warming but also to an increase in  
54 anthropogenic pressure <sup>10-12</sup>. The proliferation of these invasive microorganisms leads to  
55 eutrophication of the water bodies, intoxication of native organisms and decreasing ecosystem  
56 lakes' services <sup>13-16</sup>. Phytoplankton and particularly cyanobacteria blooms are currently  
57 observed in thermokarst lakes and will occur more frequently in the future due to global  
58 warming <sup>17-21</sup>. Indeed, main factors influencing the growth of cyanobacteria are light,  
59 temperature and dissolved and suspended nutrient composition of the medium<sup>22</sup>. Arctic regions  
60 can meet all those favorable conditions, naturally subjected to long period of sunshine during  
61 summer season. The current global warming will increase global temperature and intensify  
62 temperatures rise, especially in those regions where its impact is twice time faster than in other  
63 regions of the world (e.g., arctic amplification phenomenon <sup>23,24</sup>). In addition, massive  
64 permafrost thaw leads to the mobilization of nutrients from frozen peat layers <sup>25,26</sup> ; this is  
65 especially true in the case of dispersed peat ice, which contains a sizable amount of low  
66 molecular weight (and hence, potentially bioavailable forms) of dissolved organic matter  
67 (DOM), phosphates, macro- and micro-nutrients <sup>27,28</sup> and carboxylic acids<sup>29</sup>. These compounds  
68 can become suitable substrates for cyanobacterial development, given that cyanobacteria are  
69 capable to grow heterotrophically <sup>30-32</sup> (mixotrophic combination of auto and heterotrophy).  
70 Furthermore, it has been reported that post-wildfire precipitations increase the exports of  
71 nutrient-enriched waters from burned areas <sup>33-35</sup> which can also lead to cyanobacterial blooms  
72 and eutrophication <sup>33,36,37</sup> in temperate regions. In the high latitudes, these blooms can lead to a  
73 net autotrophic status of thermokarst water bodies during summer periods <sup>38</sup>.

74 One such cyanobacterial species is *Microcystis aeruginosa*, which is the most common  
75 genus forming freshwater cyanobacterial blooms<sup>39</sup> and the most common genera associated  
76 with toxic blooms<sup>22</sup>. Its occurrence has already been noted in the Arctic/subarctic settings near  
77 human activities, such as in Imandra Lake (Northern Europe) used as a cooling reservoir for a  
78 nuclear power plant and for technical and drinking water supply<sup>40</sup>, in sub-arctic lakes near  
79 Saint Petersburg<sup>41</sup>, in Baltic sea<sup>42</sup>, as well as in other environments, from pristine to urban areas  
80 through agricultural and industrial zones<sup>43</sup>. The potential presence of *M. aeruginosa* in Arctic  
81 and subarctic waters, the increasing number, frequency and extent of wildfires in those regions  
82<sup>44,45</sup>, and the favorable temperatures of surface waters reached during summer period could lead  
83 to significant eutrophication. Despite the importance of this process, the environmental factors  
84 controlling the proliferation of *M. aeruginosa* (temperature, insolation, inorganic nutrients,  
85 dissolved organic matter) in Arctic and subarctic regions remain poorly constrained. Such a  
86 lack of knowledge prevents foreseeing changes in thermokarst lakes' cyanobacterial  
87 development, and notably assessing the future status of these lakes, *i.e.*, a possible switch from  
88 a net heterotrophy (CO<sub>2</sub> emission to the atmosphere) to a net autotrophy (CO<sub>2</sub> uptake)<sup>8,38</sup>. Note  
89 that the C emission/uptake status of thermokarst lakes is one of the cornerstones of climate  
90 warming's impact on the Arctic and subarctic water bodies<sup>7</sup>, allowing us to respond to the  
91 question "Is there a positive or negative feedback of aquatic carbon (C) cycle to water  
92 temperature rising and permafrost thaw?". Mains hypothesis are that *i*) both rising water  
93 temperature and enhanced delivery of nutrients from frozen peat might trigger massive  
94 phytoplankton bloom and *ii*) that the increase of tundra primary productivity will lead to  
95 enhanced delivery of nutrients from plant litter leaching.

96 Towards better constraining the environmental factors governing cyanobacterial growth  
97 in DOM-rich thermokarst lakes of permafrost peatlands, we performed laboratory growth  
98 experiments using a typical invasive cyanobacteria, *M. aeruginosa*, and a series of natural

99 substrates, which are abundant in permafrost peatlands for which thermokarst lakes are fed by  
100 precipitation (surface runoff) and shallow subsurface water input. To model the main sources  
101 of nutrients in those surface waters, we used aqueous leachates of peat (permafrost and active  
102 layer) that can be the source of nutrients delivered *via* supra-permafrost flow, and tundra  
103 vegetation (lichen and moss) that can deliver nutrient *via* runoff, together with original  
104 thermokarst lake water, which combines nutrients from various sources. By encompassing a  
105 large variety of natural DOM, we specifically aimed to (1) quantify the DOM uptake by  
106 growing cyanobacteria; (2) identify the most suitable organic substrate for the growth of *M.*  
107 *aeruginosa*, and (3) apply the obtained results for estimating the consequences of permafrost  
108 thaw and water warming up on the carbon cycle in water bodies in these regions.

## 109 **2. Materials and Methods**

### 110 *2.1. Cyanobacteria origins and culture*

111 The cyanobacterium *Microcystis aeruginosa* (strain PMC 730.11) was obtained from  
112 the National Natural History Museum (MNHN) in Paris. The strain used in this experiment  
113 does not produce the microcystin cyanotoxin. Prior to the experiment, the cells were cultured  
114 in a Z8 media (see details in **Figure S 1**) on a shaker under continuous light, at room temperature  
115 (~20-25°C) and continuous air bubbling system for 7 days. At the end of the exponential –  
116 stationary growth stage and prior to the experiments with natural substrates, cyanobacteria were  
117 centrifuged to concentrate the biomass and rinsed 3 times using Milli-Q water to remove any  
118 leftover of the Z8 culture broth and cell exometabolites. The development of cyanobacterial  
119 biomass was monitored *via* measurements of the optical density at 680 nm (OD<sub>680</sub>).

120

121           2.2. *Substrate: origins and use*

122           Organic substrates used in this experiment (ground vegetation, peat from the active layer  
123 and permafrost, and thermokarst lake water) were collected in the Bolshezemelskaya Tundra  
124 zone of North-East Europe (discontinuous permafrost area, see the description given in another  
125 article <sup>46</sup>). All solid substrates were collected in the vicinity of the thermokarst lake. Vegetation  
126 involved moss (*Sphagnum angustifolium*) and lichen (*Cladonia stellaris*) samples. Both of  
127 these species are representative of boreal peatland ecosystems <sup>47</sup> and their occurrence depends  
128 on the microtopography of the peatland. Lichens are mostly spread on frozen mounds while  
129 mosses mainly occur in depressions <sup>48</sup>. Peat was collected at two different depths: i) under the  
130 first 2 cm of organic litter, within the active (unfrozen) layer, and ii) underneath the active layer  
131 within the beginning of the permafrost (frozen horizon), *i.e.* between 30 to 40 cm depth. The  
132 lake water was collected from a thermokarst lake (area of 1000 m<sup>2</sup>) and filtered on-site using a  
133 sterile Millipore filtration unit (< 0.45 µm, Merck, France).

134           For all incubation experiments, we used only liquid substrates, *i.e.* aqueous leachates of  
135 solid substrates described above (peats and vegetations). To prepare the leachates, the solid  
136 phase reacted with sterile MilliQ water (10 g<sub>dry</sub> L<sup>-1</sup>) in aerobic conditions at room temperature  
137 and under gentle mixing on a shaker. After 3 days of reaction, the suspension was centrifuged  
138 at 4,500 g, filtered through a single use 0.45 µm Nalgene Rapid-Flow sterile filter units (Thermo  
139 Fischer Scientific, France), and then used as a substrate in the experiment. Initial DOC  
140 concentration in the leachates ranged between 10 and 60 mg L<sup>-1</sup>, consistent with that occurring  
141 in natural thaw ponds and depressions of the permafrost zone (10-100 mg L<sup>-1</sup>) <sup>49,50</sup>.

142

143           2.3. *Incubation and sampling*

144           A scheme of the incubation set-up is given in **Figure 1**. Two types of reactors were  
145 used: reactors with added cyanobacteria named “experimental reactors” (ER) and reactors

146 without added cyanobacteria (*i.e.*, control experiment) called “control reactors” (CR), both  
147 placed under the same conditions.

148 Sterile 500 mL glass bottles with 300 mL of substrates were used as CR for each type  
149 of substrate. In ER, a homogeneous suspension of the cyanobacteria was transferred into 500  
150 mL sterile glass bottles, with substrates (300 mL) to obtain initial bacterial biomass of 1 g<sub>wet</sub> L<sup>-1</sup>.  
151 <sup>1</sup>. Because of acidic conditions of most leachates, not favorable for cyanobacterial growth, the  
152 initial pH of ER (prior to cyanobacteria addition) was adjusted between 5 and 6.5 using NaOH  
153 solution (1N concentration). Experimental reactors were run in duplicates for each substrate.  
154 Although it is common in biological experiments to use 3 to 5 replicates, we chose to run only  
155 two replicates per substrates ER. In this configuration, all substrates (ER and CR) were run at  
156 the same time to avoid *i*) variation of the “quality” of laboratory *Microcystis aeruginosa* strain,  
157 *ii*) incubation temperature and luminosity variations, and also *iii*) for practical reasons of  
158 sampling and analysis. Former works of our group in single bacterial culture experiments with  
159 various natural substrates demonstrated adequate reproducibility of such laboratory growth  
160 experiments<sup>20,51–56</sup>.

161 Experimental (ER) and control (CR) reactors were placed under identical conditions *i.e.*,  
162 aerated (the aeration was achieved *via* Biosilico® porous stoppers ; Thermo Fischer Scientific,  
163 France), continuous light exposure and at 25 °C, which is an ideal growth temperature for  
164 cyanobacteria<sup>57</sup>. Note that such a temperature is frequently reached in thermokarst lakes waters  
165 of permafrost peatlands during summer<sup>1,2,6,46</sup>. To avoid the formation of cyanobacterial  
166 aggregates at the bottom of the reactor, the suspension was stirred by a magnetic bar placed in  
167 each reactor. A summary of the different types of reactors and substrates used in this experiment  
168 is provided in **Table S 1**.

169 Note that, because natural leachates and lake water were filtered through a 0.45 µm and  
170 not 0.22 µm pore size, they might contain their own native microbial community<sup>58</sup> (*i.e.* pico-,



171 nano- and a part of micro-phytoplankton). However, the amount of these “native” bacteria cells,  
172 present in natural substrates and reported in literature, was several orders of magnitude lower  
173 ( $10^4$ - $10^5$  cell mL<sup>-1</sup>)<sup>6,46,59</sup> than the initial concentration of *M. aeruginosa* (1 g<sub>wet</sub> L<sup>-1</sup>), > 10<sup>9</sup> cell  
174 mL<sup>-1</sup> used in incubations.

175

#### 176 2.4. Analyses and treatment of experimental results

177 Prior to the experiment, visual and UV-range absorbance of aquatic substrates were  
178 measured between wavelength 200 and 800 nm, with a step of 1 nm. This allowed the  
179 calculation of the Weight-Average Molecular Weight index in Da units (WAMW)<sup>60</sup> and the  
180 specific UV absorbance index at 254 nm in L mg C<sup>-1</sup> m<sup>-1</sup> (SUVA<sub>254</sub>)<sup>61</sup> which was used to assess  
181 the aromaticity of samples.

182 The experiments were terminated at different times of incubation, depending on the  
183 amount of days needed to reach a steady state of cyanobacterial development (*i.e.* 13, 14, 16,  
184 and 16 days for lake water, moss, lichen, and permafrost peat leachate incubations, respectively)  
185 with the exception of the active layer peat leachate that was incubated over 29 days to achieve  
186 the decline of the cyanobacterial population. A scheme of analyses performed on each sample  
187 collected during incubation is presented in **Figure 1**. First, we sampled a homogenous  
188 suspension of 10 mL from each reactor (under shaking). A non-filtered 4 mL aliquot was used  
189 to measure pH (uncertainty of ± 0.01 pH units), conductivity (± 0.1 µS cm<sup>-1</sup>) and optical density  
190 at 680 nm (OD<sub>680</sub>). The 680 nm wavelength was chosen to be a proxy of the cyanobacterial  
191 biomass as this wavelength represents a spike in the absorbance spectrum of this cyanobacteria  
192 <sup>62</sup> and as no overlap was observed at this wavelength between all substrates and the  
193 cyanobacterial signal (tests done prior to the incubations). An aliquot of 6 mL was centrifuged  
194 at 4500 g for 15 min and the supernatant was filtered through 0.45 µm before the measure of  
195 UV absorbance at 254 nm (using a 10 mm quartz cuvette on a SpectroFlex spectrophotometer;

196 series 6600 – WTW). Dissolved organic and inorganic carbon (DOC and DIC) concentrations  
197 in the filtrates were measured *via* Shimadzu TOC-VSC, with an uncertainty of 3%. Absorbance  
198 at 254 nm wavelength has been defined as the best proxy for surface water DOC<sup>63,64</sup> and the  
199 calculated SUVA<sub>254</sub> index was used to assess the aromaticity of samples during the experiment.

200 Three indices were used to treat the results of the experiments: *i*) the total growth *ii*) the  
201 apparent growth rate and *iii*) the DOC loss during the experiment. To estimate the total growth  
202 and normalize the results, thus allowing the comparison between each substrate, we calculated  
203 the percent of growth since the day 0 of the experiment:

$$204 \text{Growth}_t(\%) = (OD_{680-ER_t} - OD_{680-ER_{t=0}}) \times \frac{100}{OD_{680-ER_{t=0}}} \quad (1)$$

205 where  $t$  represents the time of incubation. Apparent growth rate on each substrate was calculated  
206 using a linear regression of the percent growth versus elapsed time of incubation, between the  
207 last day of the adaptation phase to the last day of the exponential phase. Finally, the DOC loss  
208 in ER was calculated relative to the initial conditions (day 0 of incubation) and subtracting the  
209 DOC concentration in the control reactors from that in the experimental reactor at each  
210 sampling time of the experiment:

$$211 \text{DOC}_{loss_t} = (DOC_{ER_{t=0}} - DOC_{CR_{t=0}}) - (DOC_{ER_t} - DOC_{CR_t}) \quad (2)$$

212 where the units of  $\text{DOC}_{loss_t}$  and DOC concentration are  $\text{mg L}^{-1}$  and  $t$  corresponds to the time  
213 of incubation.

### 214 3. Results and Discussion

#### 215 3.1.M. aeruginosa growth on different substrates

216 The growth of *M. aeruginosa* in the presence of each substrate followed the same pattern  
217 summarized in three main phases: adaptation, exponential growth and death (**Figure 2**). The  
218 biomass development began with an adaptive period of time, which lasted between 20 (lake

219 ER) to 68 hours (lichen and permafrost peat ER) and was characterized by a weak decrease of  
220 the cyanobacterial biomass. This period was followed by the exponential phase, during which  
221 the population already adapted to the new conditions of the experiment and showed an increase  
222 in biomass. This exponential phase lasted between 12 and 14 days (depending on the substrate).  
223 The last phase could be monitored only for the active layer peat leachate. It consisted of the  
224 decline of the population (the death phase), and lasted about 13 days.

225 The highest growth rate was achieved for the lichen leachate at 11 % biomass per hour between  
226 day 3 and day 16 of incubation (**Table 1**). The growth rates in substrates followed the order  
227 “lichen > active layer peat > permafrost peat > moss > thermokarst lake water”, with a minimal  
228 growth rate at 2.2 % h<sup>-1</sup> for the lake water. Such differences in growth rates can be tentatively  
229 explained by phenomena described in literature. Indeed, in natural settings, many factors can  
230 inhibit the growth of cyanobacteria, such as a lack of nutrients, excessive light intensity<sup>65</sup>,  
231 water temperature<sup>57</sup> and the presence of toxic metals (Pb, Ni, Cd, Co, Zn)<sup>66</sup>. On the other hand,  
232 nutrient-rich and turbid water can promote cyanobacterial growth<sup>65,67</sup>. The presence of humic  
233 and fulvic acids (Ha and Fa) can be also beneficial for cyanobacteria, because these compounds  
234 are capable of chelating the dissolved metals<sup>66</sup>, thus alleviating their toxicity as well as  
235 increasing the bioavailability of essential micro-nutrients. We hypothesize that the combination  
236 of Ha and Fa, exhibiting high metal binding capacity, could be responsible for the difference in  
237 the impact of different substrates on cyanobacterial growth rate. Indeed, the presence of both  
238 Fa and Ha (WAMW respectively between 600 to 1000 Da, and between 1500 to 5000 Da)<sup>68,69</sup>  
239 at the pH of their maximal metal binding capacity (5-6 and 7-9, respectively)<sup>68</sup> can render  
240 lichen, moss, active layer peat and permafrost peat leachate to be highly suitable substrate for  
241 *M. aeruginosa* growth, especially at the beginning of experiment.

242           Considering thermokarst lake water substrate, weak growth of *M. aeruginosa* can be  
243 explained by a competition with native phytoplankton (pico-, nano- or micro-phytoplankton

244 originated from 0.45  $\mu\text{m}$  filtrated substrates leachates and filtrated lake water) that could have  
245 outcompeted the introduced *M. aeruginosa* population. This hypothesis is supported by quick  
246 increase of pH during the first two days of the experiment in the lake CR (**Figure 3**), which  
247 could be a sign of a photosynthetic process as also evidenced from the pH evolution described  
248 below.

249

### 250 *3.2. Chemical and biological consequences of cyanobacterial growth*

251 The pH evolution demonstrated an abrupt, over 2 to 3 units, rise during the first several  
252 days of exposure (**Figure 3**). The maximal pH value, 10.0 to 10.3, was achieved in experiments  
253 with lake water, moss and active layer peat leachates (**Figure 3A**). Note that in control  
254 experiments, there was also some pH increase (**Figure 3B**), although the steady-state pH value  
255 was 2-3 units lower than that in experiments with *M. aeruginosa*. Student test indicate that mean  
256 differences between pH values of CR and ER (from each organic substrate) are significant  
257 except for moss and lichen substrates (**Table S 2**). It is thus not excluded that some amount of  
258 native cyanobacteria initially present in the substrates were photosynthesizing in the control  
259 reactors as well. Note that, after approximately 7 days at the steady-state (stationary growth)  
260 conditions, the pH of the active layer peat leachate ER decreased from 10 to 7, which was most  
261 likely linked to cell lysis and cessation of photosynthesis.

262 Photosynthetically induced pH rises in experiments with added cyanobacteria (**Figure**  
263 **S 2**) led to a sizable increase in DIC concentration, given that the reactors were open with  
264 respect to the atmosphere and thus atmospheric  $\text{CO}_2$  could be dissolved in alkaline fluids <sup>70</sup>  
265 (**Figure S 3**).

266 The DOC concentration generally decreased starting from the very beginning of incubations  
267 (**Figure 4**). The maximal loss of DOC ( $81.8 \pm 1.0 \text{ mg L}^{-1}$ ) was achieved at the 5<sup>th</sup> day of

268 incubation in the moss ER. Maximum losses of DOC over the first 3 days in active layer peat,  
269 lichen and permafrost peat ER were  $29.5 \pm 1.0$ ,  $11.1 \pm 0.6$  and  $1.1 \pm 0.1$  mg L<sup>-1</sup> respectively. It is  
270 noteworthy that the control experiment also exhibited some decrease in DOC concentration  
271 during entire incubation time. This decrease was less pronounced in permafrost peat and lake  
272 CR (less than 2.9 mg L<sup>-1</sup> loss of DOC) but 10 times higher in moss CR (up to 111 mg L<sup>-1</sup> lost  
273 in 14 days of incubations) than in active layer peat and lichen reactor (~12 mg.L<sup>-1</sup> DOC loss in  
274 16 days) (**Figure S 4**).

275 The SUVA<sub>254</sub> was the highest in peat leachates and lake water, and demonstrated an  
276 increase over the first 3 to 5 days of incubation (**Figure 5**). Such an increase may indicate the  
277 uptake of optically-transparent, non-aromatic DOM by *M. aeruginosa*. Preferential uptake of  
278 aliphatic compounds is known for the case of growth of other, non-invasive cyanobacteria such  
279 as *Synechococcus* on moss leachate<sup>71</sup>. These authors reported that both autotrophic and  
280 heterotrophic aquatic bacteria growing on moss leachate preferred not humic-like DOM, but  
281 rather complex aliphatic and carboxylic acids. Note that some polyuronic acids such as decay-  
282 resistant sphagnum (which is known to suppress microbial activity<sup>72,73</sup>) may remain in solution  
283 and contribute to the rise of SUVA<sub>254</sub> in the course of experiments. Overall, these observations  
284 are consistent with former results that the soil and peat DOM are much less biodegradable than  
285 the aquagenic DOM<sup>74</sup>. Note that a decrease of SUVA<sub>254</sub> towards the end of experiment (**Figure**  
286 **5**), and the slight increase in DOC after 10 days of experiment with peat and moss leachate  
287 (**Figure 4**) could reflect a production of exometabolites of cyanobacteria, as well as cell lysis  
288 which occurred at the declining stage of microbial development<sup>52,71</sup>.

289

### 290 3.3. Pattern of cyanobacterial growth in active layer peat leachate ER

291 While other substrates experiments were stopped when a steady state of biomass  
292 concentration was reached, the active layer peat ER was kept running for 29 days to monitor

293 all the growth phases of the cyanobacterium and assess the changes in physicochemical  
294 parameters of the medium. As described in *section 3.1*, the growth of *M. aeruginosa* displayed  
295 the same pattern in all ER, and included the adaptation and the exponential phases, followed by  
296 the death phase (**Figure 6**). The discussion below will focus on the case of active layer peat,  
297 because it is believed that the same behaviors are observed in all phases of other substrates.

298 The adaptation phase in experiments with active layer peat lasted for 44 hours, during which  
299 the OD<sub>680 nm</sub> dropped by 17 % h<sup>-1</sup> (**Figure 6A**) and the DOC concentration decreased by 39%  
300 (from 55 to 22 mg L<sup>-1</sup>, **Figure 6B**). This decrease is believed to be the result of DOC  
301 biodegradation by the native heterotrophic microbial community as well as some heterotrophic  
302 growth of cyanobacterium<sup>71</sup>. During this first phase, the SUVA<sub>254</sub> reached 3.9 ±0.4 L mg C<sup>-1</sup>  
303 m<sup>-1</sup> (**Figure 6C**) and the pH remained stable (~6.8) (**Figure 6D**). The combined decrease of  
304 DOC and increase of SUVA<sub>254</sub> indicated a relative increase of aromatic carbon compounds due  
305 to preferential biodegradation of aliphatic DOC. The second phase corresponds to an  
306 exponential phase that lasted for 335 hours and during which the biomass of cyanobacteria  
307 almost tripled (**Figure 6A**). The associated photosynthesis led to a drastic increase in pH from  
308 6.8 to 9.6 with a maximum value reached after 209 hours of incubation (~10.3) (**Figure 6D**).  
309 Concurrently, the DOC concentration increased by 11% between 44 (end of adaptation phase)  
310 and 379 hours of exposure (**Figure 6B**) and SUVA<sub>254</sub> decreased from 3.9 to 2.6 L mg C<sup>-1</sup> m<sup>-1</sup>  
311 during this period (**Figure 6C**). The lysis of a part of *M. aeruginosa* cells are believed to be the  
312 cause of the observed DOC increase. This provided new non-aromatic organic carbon to the  
313 reactor leading to the relative decrease of SUVA<sub>254</sub>. The death phase was characterized by a net  
314 decrease of OD<sub>680</sub> (decline rate of -5.9 %·h<sup>-1</sup>, **Figure 6A**), a slight increase of DOC (gain of  
315 10%, **Figure 6B**), a decrease of SUVA<sub>254</sub> (from 2.6 to 2.0 L mg C<sup>-1</sup> m<sup>-1</sup>, **Figure 6C**) and a pH  
316 drop from 9.6 to 6.8 (**Figure 6D**). During this phase, cell lysis induced both the pH drop due to

317 the reduction of photosynthesis, and the DOC increase due to the release of cell content such  
318 as cytoplasmic and various organic compounds to the aqueous solution <sup>20</sup>.

319

320 *3.4. Carbon capture potential during M. aeruginosa growth on natural organic*  
321 *substrates and comparison with CO<sub>2</sub> evasion from thermokarst lake waters of*  
322 *permafrost peatlands*

323 Over 15 days of incubation, the biomass of *M. aeruginosa* increased by a factor of 1.5  
324 to 2, depending on the identity of the organic substrate (**Figure 2**). This translates into 1.5 to 2  
325 g<sub>wet</sub>.L<sup>-1</sup> produced during 10 to 15 days of incubation. Using results of the present laboratory  
326 experiment and considering that the wet : dry biomass ratio of cyanobacteria is 8 to 10 <sup>75,76</sup>, and  
327 that the carbon proportion in dry biomass is about 50%, the C uptake rate during cyanobacterial  
328 growth ranges between 5 and 8.3 mg C L<sup>-1</sup> d<sup>-1</sup>. By applying these results obtained under  
329 laboratory conditions to observations made in natural environment, and considering that the  
330 photic layer depth of surface waters in organic-rich permafrost peatlands is 0.5 to 1.0 m <sup>6,77</sup>,  
331 cyanobacterial growth over 2-weeks bloom period in the lake could create a C sink ranging  
332 between 2.5 and 8.3 g C-CO<sub>2</sub>.m<sup>-2</sup>.d<sup>-1</sup>. Such a high uptake rate can offset the net heterotrophic  
333 status of thermokarst lakes (> 1000 m<sup>2</sup> area) in the permafrost peatlands (currently emitting  
334 between 1 and 2 g C-CO<sub>2</sub>.m<sup>-2</sup>.d<sup>-1</sup>) <sup>6,8</sup>. Therefore, during relatively short periods of summer  
335 bloom, invasive cyanobacteria are capable of reversing the C balance of thermokarst lakes from  
336 CO<sub>2</sub> source to C sink. At the same time, the estimations provided in the present study should  
337 be considered as preliminary and likely conservative. The overall C balance of the aquatic  
338 systems in permafrost peatlands will strongly depend on the relative proportion of large and  
339 medium size thermokarst lakes and small thaw ponds and permafrost depressions. The latter  
340 are known to be hot spots of C emissions <sup>6</sup>, but at the same time, they are receiving the highest  
341 input of terrestrial DOM from peat, moss and lichen leaching and degradation <sup>55,56,59,77</sup>. Taken

342 together, explicit provisions for possible invasive cyanobacterial proliferation in thermokarst  
343 lakes and thaw ponds are needed for quantitative predictions of the future C exchanges with the  
344 atmosphere in surface waters of permafrost peatlands. Such provisions are currently absent in  
345 climate / biogeochemical models of permafrost regions.

346 It is noteworthy that after the bloom period, which mostly occurs in summer in Arctic and  
347 subarctic regions, the generated biomass, if not buried in mineral sediments or in the form of  
348 sapropel, may become a fresh source of labile DOM to surface waters. This newly imported C  
349 source could be degraded by light (photodegradation) and heterotrophic bacteria  
350 (biodegradation). Therefore, while during bloom period, the state of the thermokarst lake can  
351 switch from source to sink of C to the atmosphere, the post-bloom period could become a time  
352 of high OM degradation, thus creating sizable C emissions to the atmosphere, notably at the  
353 end of summer period. Verification of this possibility, however, requires further experimental  
354 and field work.

355 It is also necessary to point out that *M. aeruginosa* is a cyanobacterium that uses buoyancy  
356 ecostrategy, *i.e.* when present in the euphotic part of the water column, the cells generate large  
357 quantities of carbohydrates by photosynthesis<sup>78</sup>. These carbohydrates act as a ballast and allow  
358 the cells to sink to a darker part of the water column, where *M. aeruginosa* can consume these  
359 extra carbohydrates by respiration and/or fermentation, which allows it to re-ascend towards  
360 euphotic zone<sup>78,79</sup>. In temperate regions, it has been shown that the decline of temperature in  
361 autumn leads to the sinking of cyanobacteria towards the bottom of the lake, where they may  
362 survive the winter<sup>65</sup>. The effect of low temperature on the decrease of buoyancy capacity of *M.*  
363 *aeruginosa* in non-turbulent waters has been also demonstrated by laboratories experiments  
364<sup>80,81</sup>. It is thus possible that, in the current context of global warming, the growth and blooms of  
365 *M. aeruginosa* in thermokarst lakes could occur and lead to the dormancy of this



366 cyanobacterium in the bottom of lakes during winter therefore generating potential  
367 recolonization of summer waters by this buoyancy mechanisms.

368

#### 369 **4. Conclusions**

370 Laboratory growth of invasive cyanobacterium *Microcystis aeruginosa* demonstrated  
371 its capacity to proliferate on various organic substrates, relevant to surface waters of permafrost  
372 peatlands (lichen, moss and peat). The lichen leachate was by far the most favorable substrate  
373 for *M. aeruginosa* bloom, producing a pH rise of 2 to 3 units and a two-fold increase in cell  
374 biomass over two weeks of incubation in experimental reactors. Thermokarst lake water  
375 appeared to be less favorable for cyanobacterial growth, although not hostile. The cyanobacteria  
376 were capable of decreasing DOC concentration in aqueous leachate of organic compounds, *via*  
377 preferentially consuming non-aromatic carbon. It follows that, at the conditions of proliferating  
378 invasive cyanobacteria bloom, the C balance of thermokarst lake can be reverted from C source  
379 (currently emitting CO<sub>2</sub> to the atmosphere) to C sink, fixing organic C in the form of  
380 cyanobacterial biomass for a short period of time. However, the net effect of cyanobacteria on  
381 the net balance of C in the lake may be seasonally dependent, *i.e.* after the bloom period, all  
382 freshly created cyanobacterial biomass could be degraded and counterbalance the initial C-sink,  
383 although this possible degradation needs to be verified by further work. Furthermore, variable  
384 buoyant capacity of *M. aeruginosa* lead to surface – bottom migration allowing persisting of  
385 this bacterium in Arctic and subarctic peatlands surface waters over several seasons. Upon on-  
386 going climate warming in permafrost territories, accounting for possibility of invasive  
387 cyanobacterial blooms may become an issue of concern when foreseeing the net C balance of  
388 aquatic systems via modeling approaches.

389

390 **Data availability**

391 All research data are available with the following Mendeley data reference: DOI:  
392 10.17632/mnb2g87h6v.3

393 **Conflict of interest**

394 The authors declare no conflict of interest.

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402 **Author contributions (CRediT)**

403 **D. Payandi-Rolland:** conceptualization, investigation, visualization, writing – original draft,

404 **J. Larieux:** investigation, **L.S. Shirokova:** supervision, validation, writing – original draft, **P.**

405 **Bénézeth:** supervision, validation, writing – original draft, **O.S. Pokrovsky:** conceptualization,

406 supervision, validation, writing – original draft. All authors read and approved the final

407 manuscript.

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646 **Tables and Figures**

647 *Tables*

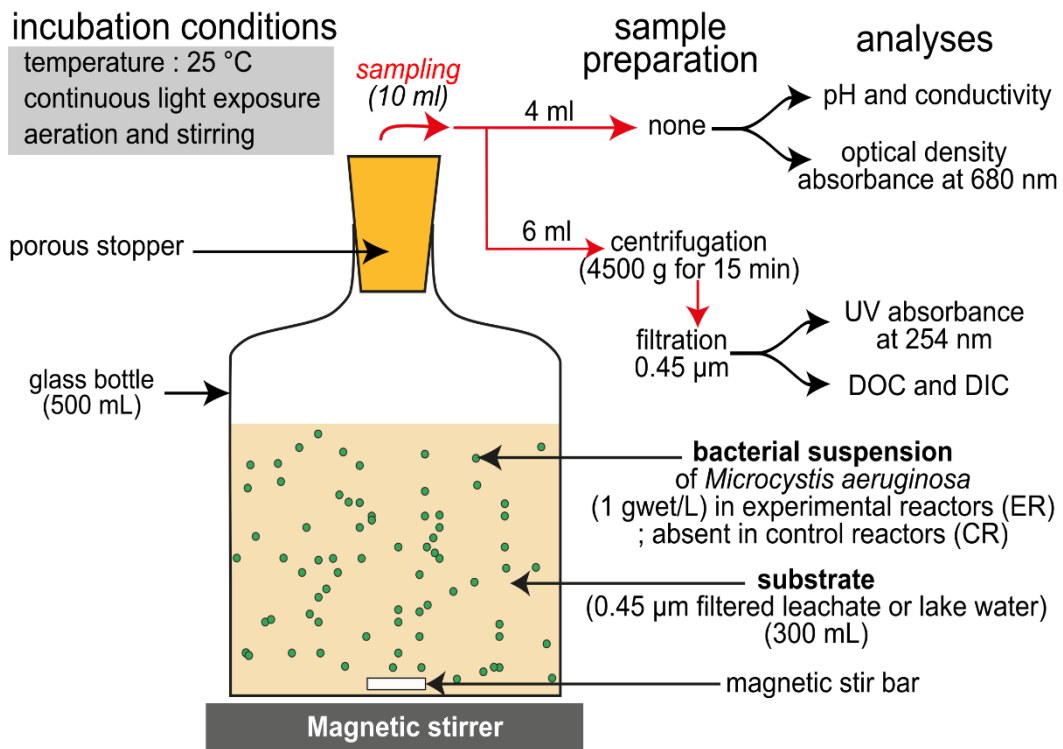
648 **Tab. 1:** Growth rates obtained by linear regression of the exponential phase in ER  
 649 (experimental reactors) incubations of all substrates, and absorbance spectroscopy index of all  
 650 substrates prior to the experiment.

Substrates	Growth rate parameters			DOM optical indices	
	Time for rate calculation, h	growth rate (% biomass h <sup>-1</sup> )	R <sup>2</sup>	SUVA <sub>254</sub> , L mg C <sup>-1</sup> m <sup>-1</sup>	WAMW, Da
moss	44-331	7.6	0.95	0.1	510
lichen	68-379	11.4	0.89	1.9	1260
active layer peat	44-379	9.6	0.97	6.0	2800
permafrost peat	68-379	8.5	0.84	8.9	4400
lake water	20-317	2.2	0.49	4.7	2300

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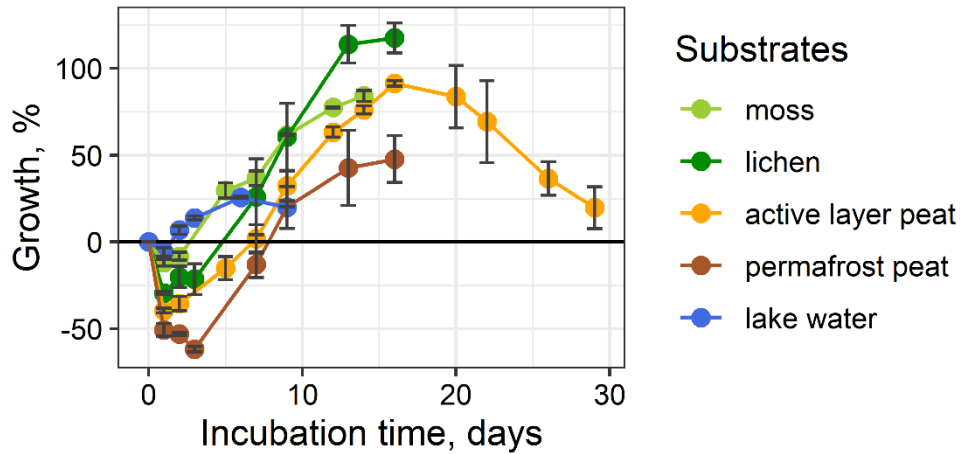
653 *Figures*



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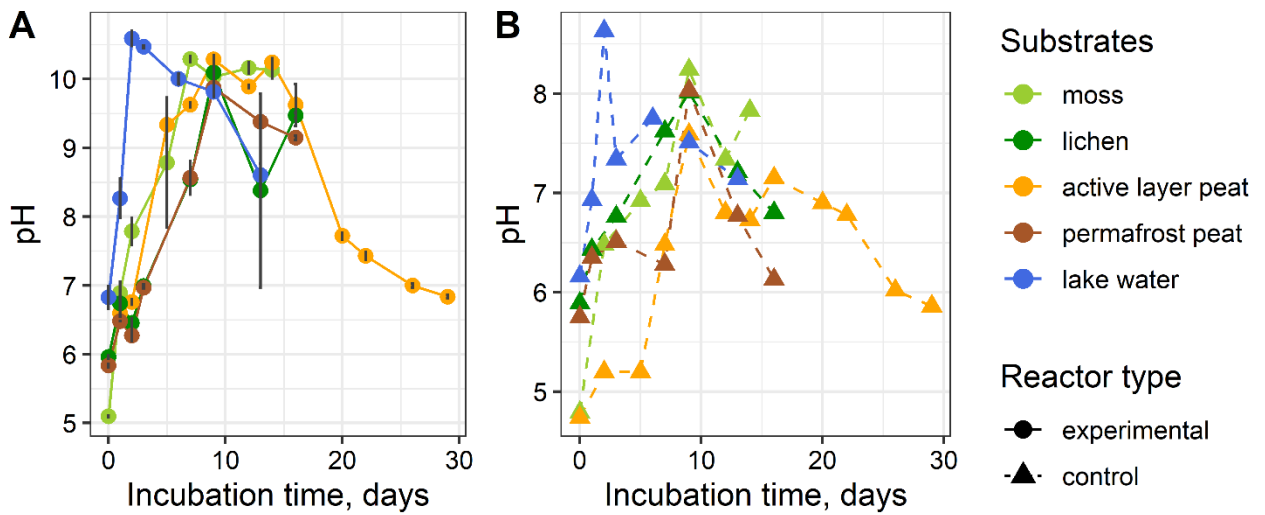
655 **Fig. 1:** Schematic of incubation set-up and various analyses performed during sampling.





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657 **Fig. 2:** Percent of growth since day 0 of the invasive cyanobacterium *M. aeruginosa* on aqueous  
 658 leachates of different organic substrates from permafrost peatlands and thermokarst lake  
 659 water. The data represent the average of duplicates with error bars of standard deviations.

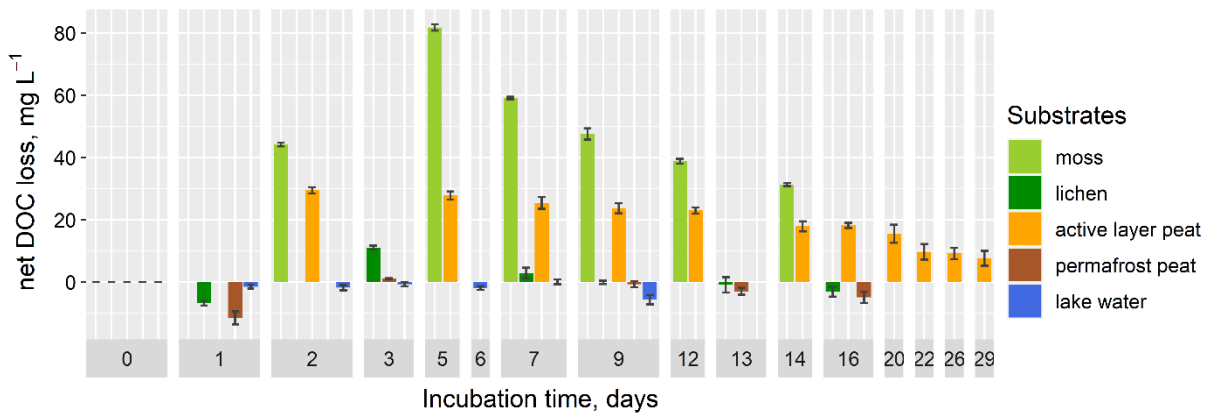


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661 **Fig. 3:** Changes of pH in experimental (with added *Microcystis aeruginosa*; **A**) and  
 662 control (**B**) reactors over incubation time.

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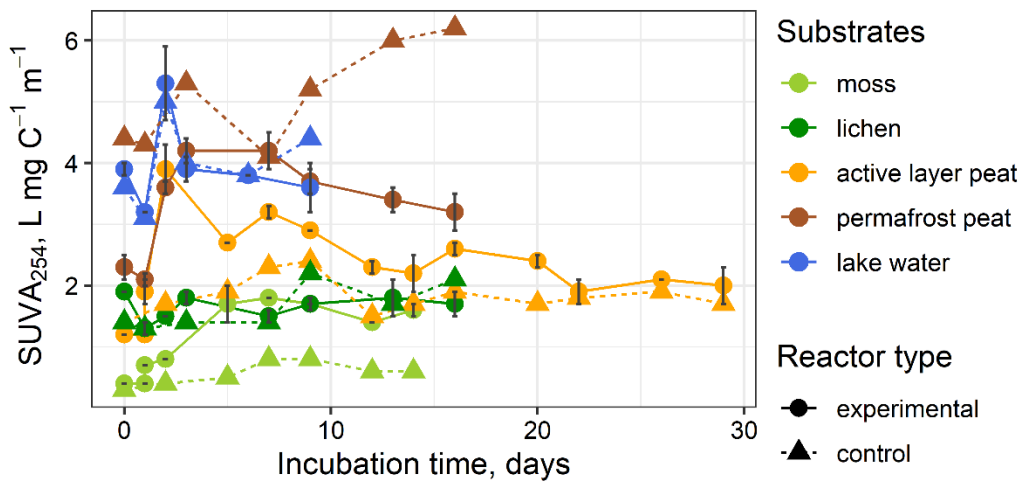


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666 **Fig. 4:** Net DOC loss for all ER (experimental reactors) during the incubation relative to  
667 DOC at day 0 of incubation (note that the DOC concentrations ER have been subtracted by  
668 the DOC concentration in the related CR (control reactors) at the same day of experiment).

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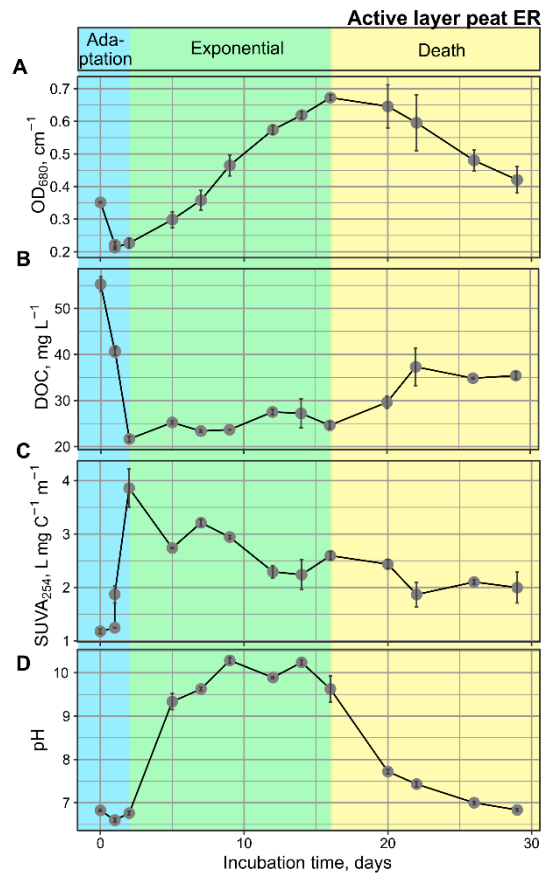
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672 **Fig. 5:** SUVA<sub>254</sub> evolution during incubation of ER (experimental reactors) and CR  
673 (control reactors).

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**Fig. 6:** Cyanobacterial growth phases in active layer peat leachate ER (experimental reactors) through 29 days of incubations and associated evolution of (A) optical density at 680 nm, (B) DOC, (C) SUVA<sub>254</sub>, and (D) pH.