**DOLICHOSPERMUM LEMMERMANNII (CYANOBACTERIA): A TEMPERATE SPECIES IN A NEOTROPICAL, EUTROPHIC RESERVOIR**

HILDA M. PALACIO¹, JAIME A. PALACIO¹, RICARDO O. ECHENIQUE², CÉLIA L. SANT’ANNA³ and JOHN J. RAMÍREZ⁴

**Summary:** Between September 2011 and October 2012, 13 samplings at 8 stations in the Riogrande II Reservoir (Colombia) were undertaken. It is located in a high-mountainous tropical (75°32’30’’ W - 75°26’10’’ W and 6°33’50’’ N - 6°28’07’’ N), which supplies water to a plant treatment for public supply and to a small hydroelectric plant. The basins of the two main tributaries of the reservoir are highly impacted by human activity. We report the presence of a Dolichospermum lemmermannii, which up to now has only been registered as a temperate and high latitude species. Also the general ecology of the species is established, such as, generation and renewal times, spatial and temporal patterns, and interaction with more important environmental variables.

**Key words:** Autoecology, ecological characteristics, potentially toxic species.

**INTRODUCTION**

Cyanobacteria are widely distributed in limnetic environments worldwide playing an essential role as primary producers in these systems. Within the group, genera of Nostocales have the capacity to fix atmospheric nitrogen, produce resistant cells, and many can regulate their buoyancy by aerotopes. Due to these and other characteristics, cyanobacteria have been able to extend their distribution and colonize environments with diversity conditions, including extreme habitats (Komárek, 2003; Aubriot et al., 2009; Sinha et al., 2012).

Over the last years, there has been an increase in the ecological information from natural and artificial continental aquatic environments from the neotropics, although the knowledge on cyanobacteria from these systems is still insufficient (Komárek & Komárková-Legnerová, 2002; Roldán Pérez & Ramírez Restrepo, 2008) and there is practically no information on the
diversity of cyanobacteria from this zone. The available studies focus on ecological aspects of phytoplanktic cyanobacteria and the use of some species in biotechnology. Cyanobacterial blooms have been reported in lakes, coastal marshes, and some reservoirs (Bula Meyer, 1985; Escobar & Manjarres, 1985; Mancera & Vidal, 1994; González et al., 2004; Correa, 2008) and is a growing problem worldwide (Codd et al., 2005; Tian et al., 2012; Elliott, 2012). In a review on South America, Dörr et al. (2010) comment that there is no data on cyanotoxins in Colombia.

*Dolichospermum lemmermannii* (Richter) Wacklin, Hoffmann & Komárek (2009), a potentially toxic species (Onodera et al., 1997; Ruge Holte et al., 1998), belongs to the traditional planktic genus *Anabaena*, currently denominated *Dolichospermum*. This genus is characterized by solitary, intercalary, and metameric heterocytes, paraheterocytic akinetes and the presence of gas vesicles in the vegetative cells (Hoffmann et al., 2005; Wacklin et al., 2009; Werner & Laughinghouse IV, 2009; O’Neil et al., 2012; Komárek & Mareš, 2012). *Dolichospermum lemmermannii* is morphologically diverse (Zapomělová et al., 2007), but akinete arrangement does not vary and is a good criterion for differentiation from other species of the genus that have different phylogenetic placements (Zapomělová et al., 2010). For this reason, the form and position of the akinetes on both sides of the heterocyte are still the only diagnostic stable characters that allow accurate morphological characterization of this species (Komárek & Zapomělová, 2007; Zapomělová et al., 2011).

The species, described in 1903 as *Anabaena lemmermannii* Richter, is commonly found in the phytoplankton of reservoirs in temperate zones (Ruge Holte et al., 1998; Olli et al., 2005; Komárek & Zapomělová, 2007; Täuscher, 2011; Cărăuş, 2012) and has not been reported for the tropical regions (Komárek & Zapomělová, 2007). In the Rio Grande II Reservoir, a population morphologically identical to *D. lemmermannii* was found. Therefore, we report the presence of this species in tropical Colombian waters and some of the ecological characteristics, such as the growth rate, generation time, and spatial and temporal disposition.

**Materials and Methods**

**Study Area**

The Rio Grande II Reservoir is located at 2200 masl in the central Andes, in northeastern Colombia, (75°32’30”-76°26’10” W and 6°33’50”-6°28’07” N). It has a T-shape form and a capacity of 253 mm³, a maximum depth of 47.2 m, and an area of approximately 1100 ha (Fig. 1). This system provides potable water to 1.4 million inhabitants of the metropolitan area of Medellín city (40% of the total population) and is also used for hydroelectric generation (up to 321MW). In this area there are typically two rainy seasons, March to May and September to November, and two dry seasons, December to February and June to August, associated to the movement of the Intertropical Convergence Zone (Franco Velásquez, 2011).

The basins of the two main tributaries of the reservoir are highly impacted, which affects their water quality. The dominant activities in this area are grazing of dairy cattle, swine industry, and large-scale tomato and potato farming. Additionally, the tributaries receive dairy farming and tanning industry discharges, as well as the wastewater of four urban centers (Bernal et al., 2005).

**Sampling and Laboratory Analysis**

Monthly, between September 2011 and October 2012, field surveys were taken at seven sampling stations (Fig. 1). Air temperature, precipitation, and solar radiation were measured using a portable weather station. In situ, using a CTD CBE Seabird Electronics profiler, water temperature, pH, electric conductivity, dissolved oxygen, and redox potential were measured. Chlorophyll a concentration was determined with a FluoroProbe bbe-Moldaenke Fluorometer.

Sub-surface water samples were taken at 10%Io (Dsd x 1.35) and 1%Io (Dsd x 2.75) using a Van Dorn bottle, using results of transparency (Dsd), estimated with a 30 cm diameter Secchi disc. This sample was used to quantify nitrates, total phosphorus, and orthophosphate (Table 1) (APHA-AWWA-WEF, 2005). In addition, 250 ml of water was sampled for taxonomic identification, counting, and biovolume estimation of *D. lemmermannii* and the other cyanobacteria.

The observation and photographs of the morphometric characteristics of *D. lemmermannii* were undertaken with a Zeiss Axioplan 2 microscope.
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![Location of the Riogrande II Reservoir and of the sampling stations.](image)

**Table 1.** Chemical variables determined in lab.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Unit</th>
<th>Method</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nitrates</td>
<td>mgN L⁻¹</td>
<td>Ionic chromatography</td>
<td></td>
</tr>
<tr>
<td>Total phosphorus</td>
<td>mgP L⁻¹</td>
<td>Colorimetric – ascorbic acid</td>
<td>4500-P-E</td>
</tr>
<tr>
<td>Orthophosphates</td>
<td>mgP L⁻¹</td>
<td>Colorimetric – ascorbic acid</td>
<td>4500-P-E</td>
</tr>
</tbody>
</table>

For determining total biovolume of cyanobacteria and of *D. lemmermannii*, 250 ml of each sample was fixed with Lugol’s solution and 50 ml sub-samples were settled in Utermöhl chambers. Counting...
was performed using a Leica DMIN inverted microscope at 400x, by the method of random fields until counting 100 individuals (colonies or filaments) of the most abundant morphotype. In cases of low densities, 60 fields were counted.

The mean cell volume of cyanobacteria was estimated from the dimensions of at least 30 cells of 30 individuals of each species, randomly selected (Hillebrand et al., 1999). To estimate the total biovolume of each taxon, the absolute density (ind/ml) was multiplied -following Ros (1979)- by the mean cell number of the colonies or filaments and by the mean cell volume.

For describing the physicochemical results of the water from the reservoir, the arithmetic mean, maximum and minimum values, and the standard deviation were used. Since the biomass data from the species did not meet the assumptions of parametric analyses, statistical significance between stations and samples was tested using c² of Friedman.

The growth rate (r) of D. lemmermannii was obtained by the cumulative biomass-time graph, which was adjusted to an exponential equation. From the growth rate (slope), the generation time (tₒ) was calculated using the expression \( tₒ = \frac{\ln 2}{r} \) and the renewal rate as the inverse of \( tₒ \). The temporal and spatial patterns of D. lemmermannii were determined by the Taylor regression potential.

Initially, with the aim of estimating the length of the gradient distribution of biomass and to determine the advisability of conducting a unimodal analysis (CCA Canonic Correspondence Analysis) or a linear (RDA-Redundancy Analysis), a DCA was performed (Detrended Correspondence Analysis) only with the biological component matrix conformed by D. lemmermannii and seven cyanobacterial phytoplankton taxa. Previously, the data was standardized. Since the gradient magnitude was 1.7, a linear RDA analysis was performed. These analyzes were performed using the CANOCO 4.0 software (ter Braak and Smilauer, 1998).

To test the significance of variance explained in the analysis of RDA through the falsification of the null hypothesis of no further effect of environment on the species, it was used a Monte Carlo simulations with 499 unrestricted permutations. The variables that were considered in the analysis recorded a value of p < 0.05 and an inflation factor < 20.

**Results**

The local precipitation (mm/day) and reservoir level (filling rate) occurring during the study period are presented in Figure 2. According to characteristics of tropical zones, the rainfall had pronounced oscillations and three periods were identified according to the values of precipitation. The samplings between September and November 2011 were characterized by high levels of precipitation, with a highest value of 40 mm/day in November. From December 2011 to February 2012 rainfall considerably reduced and starting March, the rainfall increased again to values close

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![Figure 2](image-url)  
*Fig. 2. Riogrande II Reservoir. Precipitation values (---), level of the reservoir (-----), and sampling times (—) from September 2011 to October 2012.*

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to 40 mm/day in March, April, June and higher in October 2012.

In general, changes in water level in the reservoir coincided with variations in rainfall. However, despite the decrease of rain in late November 2011 to February 2012, between September and January flooding occurred. Subsequently, from March to April 2012, the level declined to 50%, then it increased and remained stable until July 2012. Finally, we observed a decreasing trend in the level of water in the reservoir until the study was completed in October of the same year (Fig. 2).

In September, October, and December 2011 the inputs into the Grande River exceeded 60.0 m$^3$/s and highest extreme flows were reported at 70.0 m$^3$/s in October and December 2011. Only in February, August, July, and September 2012 flows in the river were lower than 10.0 m$^3$/s. Meanwhile, flows of the Chico River were relatively stable with rates lower than 20.0 m$^3$/s and fluctuated between 2.6 in September 2012 and 11.5 m$^3$/s in December 2011 (Fig. 3).

As is common in the equatorial zone, the fluctuation of shortwave radiation in the annual cycle was mild ($\text{CV}_{\text{annual}} = 18.3\%$). In contrast, there were drastic changes during a daily cycle related to cloud cover ($\text{CV}_{\text{daily}} = 80.2\%$). Air temperature varied more during a sampling than between samplings, with changes between 6.8 and 13.7 $^\circ$C during a daily cycle, because in the humid equatorial zone the temperature is more stable throughout the period (Margalef, 1974; Márquez & Guillot, 2001).

**Limnological conditions of the reservoir**

The transparency fluctuated during the study ($\text{CV} = 28.8\%$), ranging from 0.20 to 2.20 m with a mean value of $1.31 \pm 0.38$, which indicates an environment with difficulties in light penetration (Table 2). Although the extent of the photic zone reached a maximum of 6 m, the mean value was only $3.49 \pm 0.97$ m, with relatively large fluctuations ($\text{CV} = 28.0\%$). As the system was located in a tropical area, the water temperature fluctuated little during the seasonal cycle ($\text{CV} = 5.5\%$), with a mean of $20.05^\circ\text{C} \pm 1.10^\circ\text{C}$ ranging from 16.1 to 24.3$^\circ$C. The concentration of dissolved oxygen in the photic zone was always higher than 4.4 mg/L, with little variation ($\text{CV} = 14.4\%$), with a mean of 7.14 mg/L $\pm 1.03$ and levels up to 145.37% of saturation in the subsurface of the zone. While some relatively low pH values were registered, the water in the photic zone of the reservoir was generally above 8.0 at the surface and slightly varied ($\text{CV} = 7.6\%$), with a mean pH of 9.56 $\pm 0.73$. Conductivity varied between 25.7 and 74.6 µS/cm, with a mean value of 40.9 $\pm 9.67$ µS/cm.

The nutrients were in low concentrations at the photic zone in the reservoir and varied significantly over time with variation coefficients between 66.7% for the nitrates and 200% for orthophosphate. Chlorophyll a fluctuated significantly ($\text{CV} = 42.5\%$), with values of 0.30 to 50.0 µg/L and mean of 20.7 µg/L, which according to Salas & Martino (1990) indicates eutrophic conditions for tropical lakes.

![Fig. 3. Riogrande II Reservoir. Flows of Grande River (---) and Chico River (-----) and sampling times (----) from September 2011 to October 2012.](image)
Dolichospermum lemmermannii (Richter) Wacklin, Hoffmann & Komárek 2009

According to the width of the trichomes, the position and form of the akinetes, this cyanobacterium corresponds to the species described by Komárek & Zapomělová (2007) as *A. lemmermannii* Nostocales, Nostocaceae. The individuals from Riogrande II Reservoir have solitary trichomes, were irregularly coiled, and had no evident mucilage; cells barrel-shaped 4.4-8.2 µm x 4.1-5.8 µm; heterocytes more or less spherical (4.6-7.6 µm x 3.9-5.6 µm), and akinetes reniform adjacent and on both sides of the heterocyte (22.0-29.0 µm x 6.6-9.2 µm) (Table 3 and Fig. 4).

**Ecological aspects**

*Dolichospermum lemmermannii* was found in all samples in the reservoir, except in March 2012.

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Table 2. Riogrande II Reservoir. Values of physical and chemical variables measured in the photic zone, simple size (*n*), arithmetic mean and standard deviation (*m±S*), range and Coefficient of Variation (*CV, %*).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Unit</th>
<th><em>n</em></th>
<th><em>m±S</em></th>
<th>Range</th>
<th>CV (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transparency</td>
<td>m</td>
<td>206</td>
<td>1.31±0.38</td>
<td>0.20-2.20</td>
<td>28.8</td>
</tr>
<tr>
<td>Photic depth</td>
<td>m</td>
<td>206</td>
<td>3.49±0.97</td>
<td>0.55-6.00</td>
<td>28.0</td>
</tr>
<tr>
<td>Temperature</td>
<td>°C</td>
<td>206</td>
<td>20.05±1.10</td>
<td>16.10-24.30</td>
<td>5.5</td>
</tr>
<tr>
<td>Dissolved oxygen</td>
<td>mg/L</td>
<td>206</td>
<td>7.14±1.03</td>
<td>4.40-12.09</td>
<td>14.4</td>
</tr>
<tr>
<td>Oxygen saturation</td>
<td>%</td>
<td>206</td>
<td>85.72±12.43</td>
<td>53.9-145.37</td>
<td>14.5</td>
</tr>
<tr>
<td>pH</td>
<td>Units pH</td>
<td>206</td>
<td>9.56±0.73</td>
<td>6.01-10.59</td>
<td>7.6</td>
</tr>
<tr>
<td>Conductivity</td>
<td>µS/cm</td>
<td>206</td>
<td>40.91±9.67</td>
<td>25.70-74.60</td>
<td>23.6</td>
</tr>
<tr>
<td>Nitrates</td>
<td>mgN-NO$_3^{-}$/L</td>
<td>122</td>
<td>0.06±0.04</td>
<td>0.06-0.35</td>
<td>66.7</td>
</tr>
<tr>
<td>Total phosphorus</td>
<td>mgP/L</td>
<td>205</td>
<td>0.07±0.06</td>
<td>0.004-0.560</td>
<td>85.7</td>
</tr>
<tr>
<td>Orthophosphate</td>
<td>mgP-PO$_4^{3-}$/L</td>
<td>204</td>
<td>0.01±0.02</td>
<td>0.001-0.11</td>
<td>200.0</td>
</tr>
<tr>
<td>Chlorophyll-a</td>
<td>µg/L</td>
<td>185</td>
<td>20.76±8.83</td>
<td>0.30-50.24</td>
<td>42.5</td>
</tr>
</tbody>
</table>

Table 3. Riogrande II Reservoir. Comparison of the principal characteristics of *Dolichospermum lemmermannii*.

<table>
<thead>
<tr>
<th>Cells (Komárek &amp; Zapomělová, 2007)</th>
<th>Komárek (2013)</th>
<th>Riogrande II reservoir</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Form</strong></td>
<td>barrel-shaped</td>
<td>barrel-shaped</td>
</tr>
<tr>
<td><strong>Length</strong></td>
<td>2.5-10 (12,2) µm</td>
<td>4.37-8.18 µm</td>
</tr>
<tr>
<td><strong>Width</strong></td>
<td>(2.5) 4-6.9 µm</td>
<td>(2.5) 4-6.9 (7) µm</td>
</tr>
<tr>
<td><strong>Akinetes</strong></td>
<td>reniform</td>
<td>oval-cylindrical to kidney-shaped</td>
</tr>
<tr>
<td><strong>Length</strong></td>
<td>(13) 15-25.6 µm</td>
<td>(13) 15-20 (30) µm</td>
</tr>
<tr>
<td><strong>Width</strong></td>
<td>(6.3) 7.9-11 (13.3?) µm</td>
<td>(6.3) 7.9-11 (13.3?) µm</td>
</tr>
<tr>
<td><strong>Position</strong></td>
<td>either side of the heterocyte</td>
<td>singly on both sides of heterocytes (rarely on pairs)</td>
</tr>
<tr>
<td><strong>Habit</strong></td>
<td>planktonic</td>
<td>planktonic</td>
</tr>
</tbody>
</table>
Its biomass was very low in April (0.02 mm³/L) and May 2012 (0.01 mm³/L), corresponding to the period of lower waters (60% of the reservoir level) and the mean value of biomass was also low (0.56 mm³/L). The biomass presented three peaks above the mean in November 2011 (1.43 mm³/L), February 2012 (2.44 mm³/L), and June 2012 (1.22 mm³/L), thus demonstrating a high variation (CV = 134.8%) (Fig. 5A). The biomass of *D. lemmermannii* varied less in space than time (CV = 95.9%) and the highest value was found at the beginning of the arm of the Chico River (2.82 mm³/L), much higher than those found at the other sampling stations. The lowest values of this attribute were found at the end of the arm of Las Ánimas Creek (Fig. 5B).

*Dolichospermum lemmermannii* only contributed significantly to the total cyanobacterial biomass in November (56.25%) and December (27.04%) 2011 during the period of higher waters and flow of the Grande River (Fig. 2 and 3). Whereas the biomass of this species reached its highest mean value in February 2012, its contribution to the overall biomass in this month was only 8.67% (Table 4, Fig. 5A and 5B).

The results of the c² Friedman test for sampling and station factors showed significant spatio-temporal differences in *D. lemmermannii* biomass ($\alpha = 0.05$).

**Growth rate, generation and renewal times, spatial and temporal arrangement, and relationship to biological, physical and chemical variables**

While the growth rate ($r$) of *D. lemmermannii* reached 0.64 mm³/day (Fig. 5A), generation and renewal times were 1.08 (day⁻¹) and 0.93 days, respectively. In the reservoir, this species had a greater tendency to cluster in time ($b = 1.62$) than in space ($b = 0.90$). In Figures 6A and 6B the formation of three classes in time and space is evident, which are ordered from lowest to highest values of species biomass.

*Dolichospermum lemmermannii* was associated to negative quadrant in the first axis, substantially influenced by pH, temperature, transparency and level, and to the positive quadrant of second axis related to the electrical conductivity. The same taxon was negatively influenced in the first axe by rainfall, soluble phosphorus and total phosphorus (Fig. 7). In the same figure, it shows that *D. lemmermannii* is located quite close to...
other filamentous forms as *Dolichospermum* sp., *D. planctonicum*, *Sphaerospermopsis torques-reginae* and a colonial form, *Woronichinia naegeliana*. For its part, the most abundant colonial forms (*Microcystis* sp. and *M. wesemergii*) were in the opposite sector of the diagram, being heavily influenced by the concentrations of soluble phosphorus, total phosphorus and rainfall.

### Table 4. Riogrande II Reservoir. Total cyanobacterial biomass (mm$^3$/L), Total *Dolichospermum lemmermannii* biomass (mm$^3$/L) and its monthly contribution to the total cyanobacterial biomass.

<table>
<thead>
<tr>
<th>Year</th>
<th>Month</th>
<th>Biomass (mm$^3$/L)</th>
<th>Contribution of Cyanobacteria</th>
<th>Contribution of <em>D. lemmermannii</em> (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>D. lemmermannii</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Total</td>
<td></td>
</tr>
<tr>
<td>2011</td>
<td>September</td>
<td>17.879</td>
<td>0.086</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td>October</td>
<td>31.751</td>
<td>0.094</td>
<td>0.30</td>
</tr>
<tr>
<td></td>
<td>November</td>
<td>2.541</td>
<td>1.429</td>
<td>56.25</td>
</tr>
<tr>
<td></td>
<td>December</td>
<td>2.690</td>
<td>0.728</td>
<td>27.05</td>
</tr>
<tr>
<td></td>
<td>January</td>
<td>6.152</td>
<td>0.086</td>
<td>1.39</td>
</tr>
<tr>
<td></td>
<td>February</td>
<td>28.122</td>
<td>2.439</td>
<td>8.67</td>
</tr>
<tr>
<td></td>
<td>March</td>
<td>0.821</td>
<td>0.000</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>April</td>
<td>2.353</td>
<td>0.017</td>
<td>0.73</td>
</tr>
<tr>
<td></td>
<td>May</td>
<td>1.818</td>
<td>0.009</td>
<td>0.47</td>
</tr>
<tr>
<td></td>
<td>June</td>
<td>9.833</td>
<td>1.221</td>
<td>12.42</td>
</tr>
<tr>
<td></td>
<td>August</td>
<td>32.967</td>
<td>0.899</td>
<td>2.73</td>
</tr>
<tr>
<td></td>
<td>September</td>
<td>21.384</td>
<td>0.197</td>
<td>0.92</td>
</tr>
<tr>
<td></td>
<td>October</td>
<td>44.994</td>
<td>0.068</td>
<td>0.15</td>
</tr>
</tbody>
</table>

Fig. 6. Riogrande II Reservoir. (A) Biomass change rate of *Dolichospermum lemmermannii* in function of sampling time. (B) and (C) Taylor regressions for temporal and spatial scales.
The flow rates of the Grande River were considerably higher than those of the Chico River and their behavior was related to rainfall and runoff times from the basin. In a literature review, Reichwaldt & Ghadouani (2012) reported that seasonal rains changed physicochemical characteristics of aquatic environments and phytoplankton communities significantly affecting population dynamics of cyanobacteria in equatorial and tropical ecosystems.

This study demonstrated that *D. lemmermannii* biomass was low during a study period affected by the La Niña phenomenon. The entry of large volumes of water during the rainy season led to a decline in algal biomass, due to the high rates of washing (Bouvy *et al*., 2003; Figueredo & Giani, 2009) and hence the inverse relationship between *D. lemmermannii* biomass, precipitation and reservoir level (Fig. 7). In particular, the overflow water of Riogrande II Reservoir coincided with very low biomass in November and December 2011 and major changes in the flow of the tributaries and the reservoir level seem to favor increased biomass of cyanobacteria.

When planktonic algal biomass, -and in this case, of *D. lemmermannii*- increases, pH increases due to the incorporation of dissolved inorganic carbon, in particular CO$_2$ and HCO$_3$-, for photosynthesis. This process requires nutrients such as reactive soluble phosphorus and others not measured in this study, which are readily incorporated because of the high tropical temperatures that increase algal metabolism and rapid microbial assimilation of orthophosphates. Even in the presence of high loadings of phosphorus, chronically low concentrations of this nutrient are generated, which stimulates the growth of cyanobacteria with heterocytes. Simultaneously, low levels of nitrogen favor diazotrophic species (O’Neil *et al*., 2012) and, in particular, the thermal stability of Riogrande II Reservoir allows buoyant cyanobacteria to proliferate (Reynolds *et al*., 2002).

Transparency decreases due to algal self-shading, preventing light penetration. The relationship...
between conductivity and increased biomass of *D. lemmermannii* is due to the contributions of the basin and alkalinity caused by carbonates and bicarbonates present due to increases in pH.

According to the results of different trophic indices, the reservoir was considered eutrophic (Loaiza-Restano *et al*., 2011; Zabala, 2013) and therefore was expected high cyanobacterial biomass. Consequently, it is possible to assume that La Niña and the high flows by tributaries during much of the study did not allow the development of *Dolichospermum* populations with high biomass in the reservoir. Thus, in a bimodal annual cycle with typical precipitation conditions, we could expect significant changes in the cyanobacterial biomass and in particular *D. lemmermannii* in the reservoir. Although the population dynamics of cyanobacteria may be affected by multiple environmental factors, the results of the RDA are consistent with the fact that this species is found in eutrophic reservoirs (Komárek & Zapomělová, 2007; Olli *et al*., 2005; Täuscher, 2011; Cărăuş, 2012; Ruge Holte *et al*., 1998).

*Dolichospermum lemmermannii* displayed a curve of exponential growth. The mean growth rate of this species estimated in the field (1.10 d\(^{-1}\)) was higher than that reported by Reynolds (1984, 2006) for *Microcystis aeruginosa* (Kützing) Kützing (S strategist) under laboratory conditions at 20°C (0.80 d\(^{-1}\)) and R strategist *Sphaerospermopsis aphanizomenoides* (Forti) Zapomělová, Jezberová, Hrouzek, Hisem, Reháková & Komárková (0.38 d\(^{-1}\)), but lower than that of *Synechococcus* Nägeli (C strategist) with a value of 7.91 d\(^{-1}\) (Reynolds, 1984, 2006; Olrik, 1994).

The significant differences in biomass of *D. lemmermannii* in space and time (Fig. 5A and 5B), as the groups formed in these two scales (Fig. 6A and 6B) confirm the formation of patches over time, especially in February 2012 at the upper Chico River station (1.53 mm\(^3\)/L). It is possible that the volume of water contributed by the Grande River, about three times more than the Chico River, increases the residence time of water at this station and favors the accumulation of *D. lemmermannii* biomass and thus a greater degree of eutrophication (Loaiza-Restano *et al*., 2011; Zabala, 2013). Additionally, the patches were higher in February 2012 at the end of the period of low rainfall and the beginning of the decrease in the flow into the reservoir (Fig. 2 and 3).

In Figure 7 it shows that the ecology of *D. lemmermannii* is strongly influenced by: 1) the competence of filamentous taxa using the same strategy for access to resources, especially the light, and 2) the level fluctuations related with increases or decreases in rainfall and the different forms of phosphorus, especially soluble forms. Because of its location on the opposite side of the diagram, it can also be assumed that increases in biomass of filamentous taxa, as *D. lemmermannii*, decrease the biomass of colonial forms as *Microcystis*.

In many aquatic ecosystems, Huisman and Hulot (2005) observed that changing cloudy weather with occasional thunderstorms to sunny weather with a low effect of turbulence and weak vertical mixing, favors the development of cyanobacterial blooms, especially filamentous. It is well known, as reported by Olrik (1994), Reynolds (1984, 2006) and Reynolds et al. (2002), that colonial cyanobacteria as *Microcystis* type are widely affected by intense vertical mixing.

Finally, we consider that *Dolichospermum lemmermannii* can be classified as an R strategist by the characteristics of the reservoir, which are turbid, eutrophic, limited light availability, shallow, reduced mixing, reduced depth (Mazo, 2008; Loaiza-Restano *et al*., 2011), and ‘acclimitable’ tolerant mixing (Reynolds, 2006).

**Conclusions**

The Riogrande II Reservoir is an environment with a predominantly alkaline condition in the photic zone, permanently stratified, with a high mean surface temperature and a relatively narrow but well oxygenated photic zone. Although in the photic zone of the reservoir water had low concentrations of nitrates and orthophosphate, total phosphorus values were average and high for chlorophyll *a*, characteristic of eutrophic environments found.

Alkaline water conditions, the thermal stability of the reservoir, the mean high temperature, low concentrations of soluble forms of nutrients in the water show favorable conditions for the growth of cyanobacteria in the photic zone of the Riogrande II Reservoir.

Although the akinetes of the population of *D. lemmermannii* from the Riogrande II Reservoir...
have a larger maximum length and lower maximum width than those described by Komárek & Zapomělová (2007), the shape and position within the trichomes are identical.

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