Acta Bot. Croat. 77 (2), 135–140, 2018
DOI: 10.2478/botcro-2018-0010

CODEN: ABCRA 25
ISSN 0365-0588
eISSN 1847-8476

Photosynthetic performance of two freshwater red algal species

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Abstract – Photosynthetic performances of two freshwater red algal populations from freshwaters of the Carpathian basin were measured in this study. Populations were collected from different habitats: *Bangia atropurpurea* from Lake Balaton and *Batrachospermum gelatinosum* from the Tapolca stream. Their photosynthesis was studied in a wide range of temperature (5–35 °C) and light intensity (0–1150 µmol m^{-2} s^{-1}) in a photosynthetron. We found both species' photosynthesis maxima at 25 °C but *B. atropurpurea* had significantly higher photosynthetic production. Low and medium values were calculated for the species' photoadaptation parameters. Compensation light intensities determined in this study were similar to those obtained in previous studies. Both species utilized light efficiently; photoinhibition was detected only at two measuring temperatures for *Bangia* and at four measuring temperatures for *Batrachospermum*. P-T characteristics of the species revealed that both have temperature optima at 25 °C under high and medium light intensities but there are no such remarkable optima at low irradiance. The biomass specific respiration of both species increased with increasing temperature. We confirmed the good light utilization of these red algal species but found temperature optima higher than reported previously.

Keywords: *Bangia atropurpurea*, *Batrachospermum gelatinosum*, ecophysiology, light, photosynthetic characteristics, temperature

Abbreviations: P_s – maximal production obtained in the absence of photoinhibition, P^B_{max} – biomass specific maximal photosynthetic rate, I_k – photoadaptation parameter, I_c – compensation light intensity, α – initial slope of the curve, light utilization, β – photoinhibition parameter, R^B – biomass specific respiration.

Introduction

Red algae are mostly marine macroscopic organisms. Besides the 5000–5500 marine Rhodophyta species there are about 180 species living in fresh waters; most are limited to running waters. They are often considered as indicators of good water quality and clean habitats as they prefer very clear, transparent habitats (Skuja 1938, Sheath 1984). *Bangia atropurpurea* (Mertens ex Roth) C. Agardh and *Batrachospermum gelatinosum* (Linnaeus) De Candolle are filamentous red algae with worldwide distribution, commonly growing attached to the surface of shoreline rocks of lakes and streams.

Bangia atropurpurea is an unbranched filamentous red alga that grows along rocky shorelines. The species occurs both in fresh- and seawater. It was often mentioned under the name *B. fuscopurpurea* (Dillw.) till Geesink (1973) concluded that these two taxa are conspecific. *B. atropurpurea* was described in North America, Europe, the Middle East, and in Japan (Belcher 1960, Geesink 1973, Sheath and Cole 1980, Araki et al. 1994, Barinova 2013). Barinova (2013) found *B. atropurpurea* in a wide range of temperature (15.5–35 °C), pH (6.6–8.0), and conductivity (0.82–4.0 mS cm^{-1}). Temperature and day length dependence of the growth rate, maturation and size of the species were also reported (Sommerfeld and Nichols 1973). Monospore germination of *B. atropurpurea* is light-dependent (Charnofsky et al. 1982). Optimum conditions for the photosynthesis were found at 20 °C and 750 µmol m^{-2} s^{-1} (Graham and Graham 1987).

Batrachospermum gelatinosum is widely distributed in the running waters of North America and Europe. Popu-

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lations, as red algae usually, occur at cold temperatures (0–22 °C) in circumneutral (pH 6–8.5) waters with low conductivity (10–490 μS cm^{-1}) (Kremer 1983, Vis et al. 1996, Vis and Sheath 1997, Carmona et al. 2011, Chiasson et al. 2014, Drerup and Vis 2014). *B. gelatinosum* was also described in Central and South America, Australia and in the Middle East under similar conditions (Vis and Entwisle 2000, Jiménez et al. 2004, Vis et al. 2008, Barinova 2013). Besides the distribution, the physiology of some *Batrachospermum* species (*B. ambiguum*, *B. delicatum*, *B. gelatinosum*, *B. helminthosum* and *B. vogesiacum*) were also studied. It was shown that low irradiance is advantageous for the growth of red algae species. Species-specific temperature optima of the growth were established by Zucchi and Necchi (2001) and Drerup et al. (2015).

Our knowledge about the Hungarian red algae flora is quite limited. The total number of taxa recorded in Northern European countries is higher than that in Central- and South-Europe. In Hungary, nine taxa were reported (Kwandrans and Eloranta 2010), two of these (*Batrachospermum ectocarpum* Sirodot and *B. moniliforme* Roth) were found in the springs of the Northern Bakony Mountains (Kol 1968). Additionally, some species (*Audouinella ciolacea* (Kütz.) Hamel, *Audouinella chalybea*, *Chroodactylon ornatum* (Ag.) Basson, *Hildebrandia rivularis* (Lieben) Ag., *Porphyridium purpureum* (Bory) Drew et Ross, *Thorea hispida*) were reported from the two main rivers (Danube and Tisza) (Kiss and Pelyhe 2004, Szemes 1967, Uherkovich 1957). Extended stands of *Bangia atropurpurea* were described from the shoreline rocks of Lake Balaton (Tamás 1959) but, as a consequence of eutrophication, the species was suppressed in the last decades (Kiss and Pelyhe 2004). As a consequence of restoration measures (Istvánovics et al. 2007), *B. atropurpurea* reappeared in early spring, 2015 offering an opportunity to study its photosynthetic performance.

Because of our scarce knowledge about the Hungarian red algae and a lack of physiological data, measurements were carried out to determine not only the temperature and light intensity optima but also the tolerance range of the populations. For this reason, we carried out experiments in a wide range of temperature and light conditions.

Materials and methods

Two populations of freshwater red algae were investigated in this study. Samples were collected during the period of highest abundance from surfaces of stones then were kept in filtered (0.45 μm pore size membrane filter) stream or lake water depending on sampling site.

Bangia atropurpurea was collected from shoreline rocks of Lake Balaton in February 2015 (water temperature was 4.9 °C) (46°54'53.9928" N, 17°53'34.4148" E). Lake Balaton is the largest shallow lake in Central Europe, with slightly alkaline water (pH~8.3). The dominant ions of the lake are Ca^{2+}, Mg^{2+} and HCO_3^-, and Secchi transparency rarely exceeds 1 m. Long sections of the lake's shoreline are artificially covered by large red sandstone bricks to protect the shoreline constructions against wave action. These rocks provide suitable habitats for *B. atropurpurea*.

Batrachospermum gelatinosum was collected from the Tapolca stream (46°51'1.224" N, 17°25'17.8248" E) in April 2015. The stream is fed by hot springs. Its temperature varies between 9.6 and 21 °C during the year and it cools down only slightly in winter. During the sampling, water temperature was 16.1 °C. Small and medium size stones (5–15 cm) cover the streambed; red algae grew attached to the surface of this substrate.

The following physical parameters were recorded during samplings: temperature, pH, dissolved oxygen concentration, oxygen saturation and conductivity with HQ40d Portable Multi-Parameter Meter (Hach Lange) and IntelliCAL™ PHC101 Rugged Gel Filled pH Electrode, IntelliCAL™ CDC401 Rugged Conductivity Probe, IntelliCAL™ LDO101 Rugged Luminescent/Optical Dissolved Oxygen (LDO) (Tab. 1).

Photosynthesis measurements were carried out in a photosynthetron developed by Üveges et al. (2011), which allows measurements at nine different light intensities at the same time at a given temperature. Light intensities were set between 0–1150 μmol m^{-2} s^{-1} (0, 15, 35, 75, 150, 300, 600, 800, 1000 μmol m^{-2} s^{-1} were used for *Bangia* and 0, 10, 30, 75, 130, 200, 420, 1150 μmol m^{-2} s^{-1} were used for *Batrachospermum*), PAR was provided by daylight tubes (Tungsram F74). Light intensities in the different cells were measured with a spherical (4 π) quantum sensor. A wide range of temperature was used to determine not only the temperature optima but also the tolerance ranges of the species. Incubation temperature was increased by 5 °C increments in the temperature range 5–35 °C. Permanent temperature was provided by Neslab RTE-211.

Red algal samples were filtered onto 1.2 μm pore size GFC filters, and then fresh weight was measured with 0.1 mg accuracy. Known fresh weights of the field samples were placed into Karslruhe-flasks, which were then filled with fresh filtered (0.4 μm pore size mixed cellulose-ester membrane filter) stream or lake water before each measurement.

Prior to the experiments, samples were pre-incubated at least for 2 h at each measuring temperature. Photosynthetic

Tab. 1. Environmental data measured at sampling sites.

	Tapolca-stream	Lake Balaton
Collected species	*Batrachospermum gelatinosum*	*Bangia atropurpurea*
Date	20 April 2015	16 February 2015
Location	46°51'1.224"N 17°25'17.8248"E	46°54'53.9928"N 17°53'34.4148"E
Temperature (°C)	16.1	4.9
pH	7.61	8.5
Dissolved oxygen (mg L^{-1})	9.19	12.17
Oxygen saturation (%)	93.7	94.9
Conductivity (μS cm^{-1})	704	565

activity of the species were followed by measuring dissolved oxygen concentration (DO) with an IntelliCAL™ LDO101 sensor (Hach Lange). After the pre-incubation period, DO was measured at the beginning, then after 1 h and 2 h. The special design of the Karlsruhe-flasks prevents gas exchange with the environment. In the case of both species, measurements were conducted in three replicates at each of the nine light intensities.

Respiration, gross- and net photosynthesis were determined according to Wetzel and Likens (2000). Two equations were used to determine the following photosynthetic parameters of the species: biomass specific maximal photosynthetic rate (P^B_{max}), maximal production obtained in the absence of photoinhibition (P_s; without photoinhibition it is equal to P^B_{max}), photoadaptation parameter (I_k), compensation light intensity (I_c), initial slope of the curve (α), biomass specific respiration (R^B). In the absence of photoinhibition, photosynthetic parameters were calculated according to Webb et al. (1974). If photoinhibition was observed, photoinhibition parameter (β) was also calculated according to Platt et al. (1980). Curves were fitted using GraFit software (Leatherbarrow 2009). To determine the compensation light intensity (I_c), a reordered form of the equation of Webb et al. (1974) was used in each case:

$$I_C = \frac{P_S \,.\, ln\left(1 - \frac{R^B}{P_S}\right)}{-\alpha}$$

where I_c is the light intensity at which photosynthetic production becomes equal to respiration.

Results

Photosynthesis-light intensity characteristics

The biomass specific maximal production (P^B_{max}) of the species increased in parallel with the temperature (Figs. 1, 2).

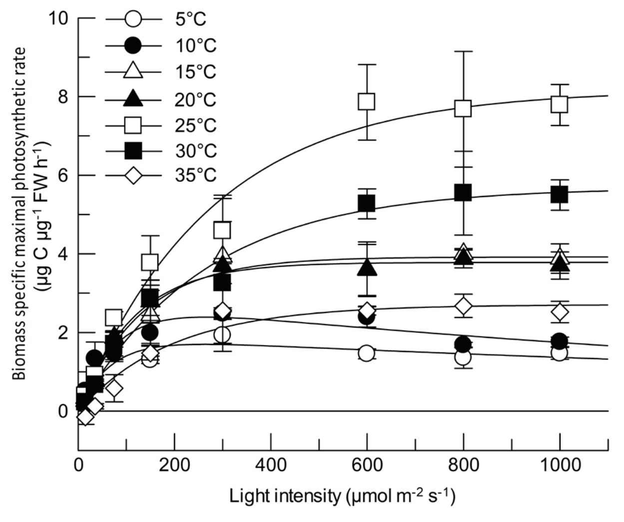

Fig. 1. Gross photosynthesis–irradiance (P–I) curves of *Bangia atropurpurea* measured along a temperature gradient. Data are average mean ± SD, n= 3.

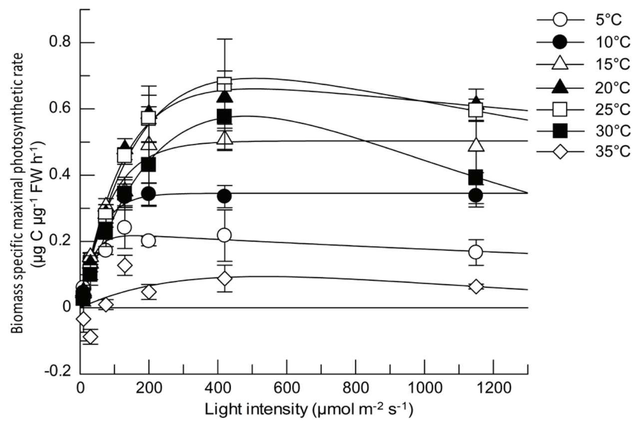

Fig. 2. Gross photosynthesis–irradiance (P–I) curves of *Batrachospermum gelatinosum* measured along a temperature gradient. Data are average mean ± SD, n= 3.

The increase of the P^B_{max} was about 75–80% for both species and both had maxima at 25 °C. A remarkable difference was found between the photosynthetic production levels of the species. The highest P^B_{max} of *Batrachospermum* was 0.683 µg C µg^{-1} FW h^{-1} in contrast to *Bangia*, which exhibited a photosynthetic production higher by an order of magnitude (P^B_{max} = 8.171 µg C µg^{-1} FW h^{-1}). At 35 °C, the highest experimental temperature, both species' photosynthetic activity dropped. The P^B_{max} of *Bangia* decreased at 35 °C but it was still remarkable. The drop in the photosynthetic activity of *Batrachospermum* was about 95%, and gross photosynthetic activity at 35 °C was detected only at five light intensities.

P_s values of *Bangia* were calculated only at 5 and 10 °C because at higher temperatures photoinhibition was not observed, and the obtained data were similar to P^B_{max}. In the P_s values of *Batrachospermum,* differences were found: contrary to P^B_{max}, P_s values increased with temperature and reached the highest value at 30 °C (1.195 µg C µg^{-1} FW h^{-1}). A decrease was observed only at the highest temperature (35 °C) but this drop was remarkable.

Photoadaptation parameters (I_k) of *Bangia* varied between 61.6 and 275.1 µmol m^{-2} s^{-1}. They increased with the increasing temperature till 25 °C. At higher temperatures a slow decrease was observed in the I_k values. I_k values of *Batrachospermum* were lower and ranged from 32 to 165.8 µmol m^{-2} s^{-1}. The highest value was found at 30 °C.

Light utilization (α) of *Bangia* decreased with increasing temperature and changed between 1.39 × 10^{-2} and 3.26 × 10^{-5} µg C µg^{-1} FW h^{-1} (µmol m^{-2} s^{-1})$^{-1}$, which means that the efficiency of light utilization of the species decreased with increasing temperature. α parameters of *Batrachospermum* also decreased along the temperature gradient: it varied from 6.8 × 10^{-3} to 9 × 10^{-4} µg C µg^{-1} FW h^{-1} (µmol m^{-2} s^{-1})$^{-1}$.

Photoinhibition (β) was not observed at any of the applied temperatures. *Bangia* showed photoinhibition at a lower part of the temperature range (5–10 °C): β was 6 × 10^{-4} and 1.5 × 10^{-3} µg C µg^{-1} FW h^{-1} (µmol m^{-2} s^{-1})$^{-1}$. In contrast, *Batrachospermum* had β values at almost each measuring temperature including the higher temperature range (20–35 °C). They varied between 4.6×10^{-5} and 1.1×10^{-3} µg C µg^{-1} FW h^{-1} (µmol m^{-2} s^{-1})$^{-1}$.

Respiration of both species increased with temperature. This increase was higher than 90% for both species. Although *Bangia* had a higher biomass specific respiration, these values for the two species were much more similar than their biomass specific productions.

Photosynthesis-temperature characteristics

Plotting the mean values of photosynthetic activity as a function of the temperature (P–T), it is possible to examine the temperature dependence of the photosynthesis at each light intensity. In the 75–1000 µmol m^{-2} s^{-1} light intensity range biomass specific productions of *Bangia atropurpurea* increased with the temperature and reached a maximum at 25 °C (Fig. 3.). Besides, at the highest temperatures (30 and 35 °C) a decrease was found. The highest level of photosynthesis was observed at 600 µmol m^{-2} s^{-1}. At lower light intensities (35 and 15 µmol m^{-2} s^{-1}) outliers were found at 10 °C.

At light intensities between 1150 and 130 µmol m^{-2} s^{-1}, the biomass specific maximal production of *Batrachospermum* showed normal distribution and had maxima at 20 and 25 °C (Fig. 4.). At 75 µmol m^{-2} s^{-1}, P^B_{max} of the species reached the highest value at 15 °C and after a slight decrease a remarkable drop was found at 35 °C. At low light intensities (30–10 µmol m^{-2} s^{-1}), P^B_{max} maxima were detected at the lowest temperature (5 °C) and a slight decrease was observed. Under low light conditions at the highest measuring temperature (35 °C), gross- and net photosynthetic activity were not observed.

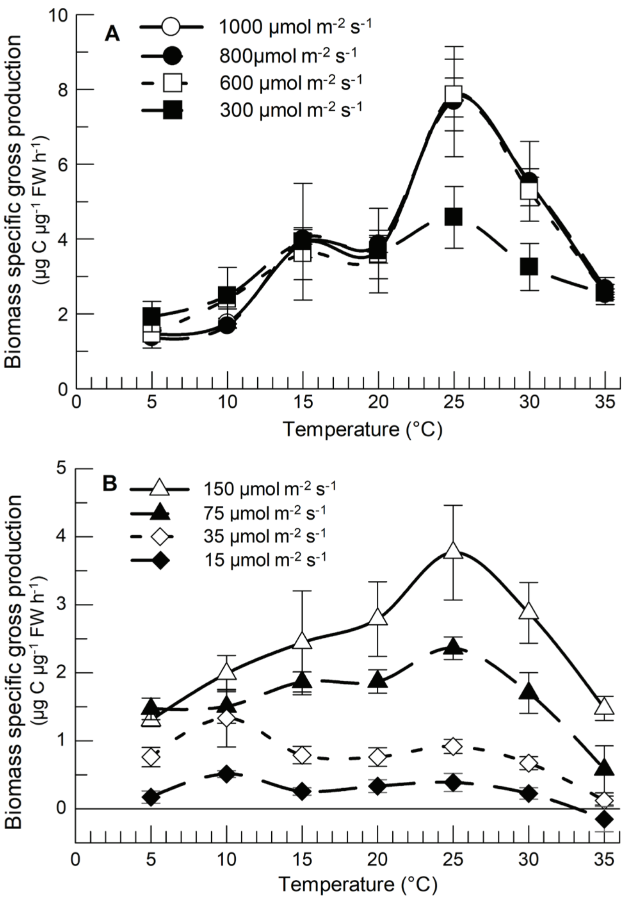

Fig. 3. Gross photosynthesis–temperature (P–T) curves of *Bangia atropurpurea* measured at high (A) and low (B) incubation light intensities. Data are average mean ± SD, n= 3.

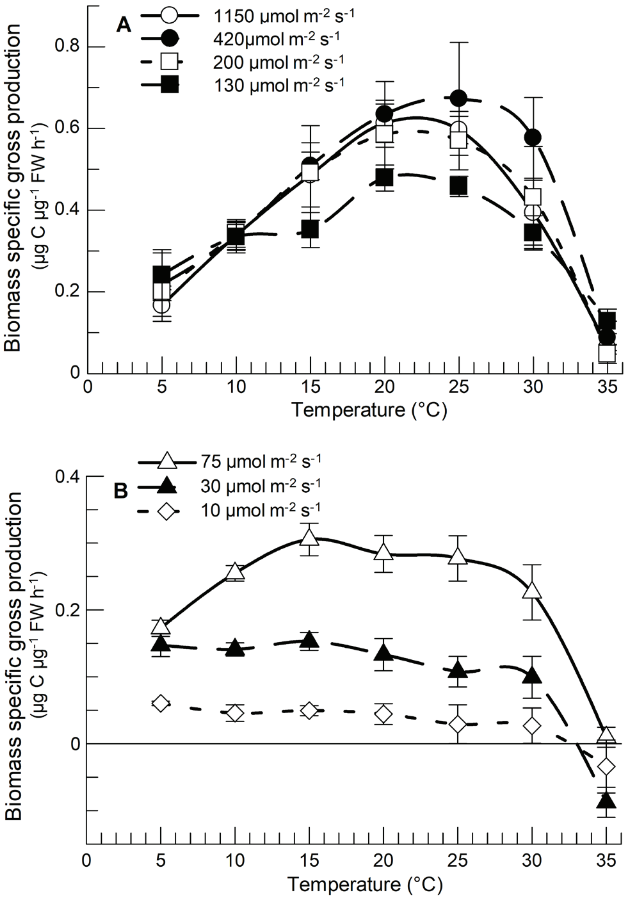

Fig. 4. Gross photosynthesis–temperature (P–T) curves of *Batrachospermum gelatinosum* measured at high (A) and low (B) incubation light intensities. Data are average mean ± SD, n= 3.

Discussion

Physiological optima of different red algal species are thoroughly studied worldwide. Temperature and light intensity optima of the different species were determined in several studies (On-line Suppl. Tab. 1). Adaptation to low light intensity and temperature has been reported both for *Batrachospermum gelatinosum* and for *Bangia atropurpurea* (Sommerfeld and Nichols 1973, Geesink 1973, Necchi and Zucchi 2001, Necchi and Alves 2005). Since previous studies applied many different and inconvertible units, direct comparisons are difficult. However, it is possible to compare trends.

In contrast to many other red algae, *Bangia atropurpurea* is a well-studied species. Low temperature and light intensity are considered the optimal conditions for the species. Because Rhodophyta species are commonly found at low temperatures and light intensities, most previous experiments were limited to low temperature and light intensity ranges (On-line Suppl. Tab. 1). In most cases, these values varied between 9–20 °C and 4–200 µmol m^{-2} s^{-1} (Belcher 1960, Geesink 1973, Sommerfeld and Nichols 1973, Sheath and Cole 1980, Charnofsky et al. 1982). Graham and Graham (1987) carried out laboratory experiments on growth and reproduction of *Bangia* in a wide range of temperatures and light intensities. Their finding that *Bangia* has a temperature optimum at 20 °C and a light intensity optimum at 750 µmol m^{-2} s^{-1} differs from previous findings as well as from our observations. The extremely high light optimum should be a result of the different data analysis. Our results regarding temperature preferences are similar to those of Graham and Graham (1987): we found a temperature optimum for photosynthetic production at 25 °C. This temperature is much higher than the usual cultivating temperatures and other findings reported previously. As to light preferences, we found a maximum of 275 µmol m^{-2} s^{-1} in I_k values at 25 °C. Light utilization of the species decreased with the increasing temperature, which suggested an acclimation to low light intensity and temperature in agreement with the previous findings (Sheath 1984). Photoinhibition was found only at low temperatures (5–10 °C) in contrast to Graham and Graham (1987). Even though they did not do the calculations, their results suggest that *Bangia* sp. had photoinhibition at elevated temperatures (20–30 °C).

Batrachospermum gelatinosum, like red algae in general, occurs in cold, clean running waters (7–14 °C), Kremer (1983), Vis et al. (1996), Vis and Sheath (1997), Drerup and Vis (2014) and we also found it under such conditions (Tab. 1). Several experiments were carried out on the photosynthesis of different *Batrachospermum* species. In accordance with our results, Kremer (1983) found a temperature optimum at 20–25 °C for the photosynthetic production of *Batrachospermum* sp. when a short temperature adaptation time was used before measurement; however, Kremer (1983) found a lower temperature optimum (15 °C) if the adaptation time was longer, and suggested that the use of a longer adaptation time is needed. Necchi and Zucchi (2001), Zucchi and Necchi (2001), Necchi and Alves (2005) and Drerup et al. (2015) investigated Rhodophyta species, including *Batrachospermum* species (On-line Suppl. Tab. 1). Zucchi and Necchi (2001) found growth optimum for *Batrachospermum* species at 20 °C along with a preference for low light intensity (65 µmol m^{-2} s^{-1}). Necchi and Zucchi (2001), Necchi and Alves (2005) and Drerup et al. (2015) conducted photosynthesis measurements at 20 °C and found differences between *Batrachospermum* species light optima for photosynthetic production. I_k values varied between 6 and 76 µmol m^{-2} s^{-1} which is lower than our findings at this temperature (122 µmol m^{-2} s^{-1}). As to compensation light intensity, I_c values varied between 2 and 16 µmol m^{-2} s^{-1} , which was similar to data by Necchi and Zucchi (2001), Necchi and Alves (2005) and Drerup et al. (2015). Confirming previous publications, we also found a high level of light utilization and photoinhibition at 20 °C (Necchi and Zucchi 2001, Necchi and Alves 2005, Drerup et al. 2015).

In comparison to ecophysiological data of species other than Rhodophyta, it is apparent that most species have photosynthesis maxima at higher temperature (e.g. Üveges et al. 2012, Pálmai et al. 2013, Lengyel et al. 2015, Pálmai et al. 2016) than these two Rhodophyta populations. Similar I_k values were found for *Microcystis aeruginosa*, *Merismopedia tenuissima* and *Oscillatoria* sp. (Coles and Jones 2000), *Porphyra* species (Lin et al. 2008), *Aphanizomenon flos-aquae* (Üveges et al. 2012), *Nitzschia frustulum* (Lengyel et al. 2015), but there are also species with lower (*Picocystis salinarum* (Pálmai et al. 2013), and with higher photoadaptation parameters, like *Arthrospira fusiformis* (Pálmai et al. 2013), *Microcystis flos-aquae* (Pálmai et al. 2016). Similarly, efficient light utilization was reported for Rhodophyta species (Necchi and Zucchi 2001, Necchi and Alves 2005, Drerup et al. 2015) but also good utilization was determined for *Aphanizomenon flos-aquae* (Üveges et al. 2012) and for *Picocystis salinarum* (Pálmai et al. 2013).

Acknowledgement

This research was supported by the Hungarian National Research, Development and Innovation Office (NKFIH K-120595).

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