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Katarzyna Możdżeń*, Patrycja Zagata Leśnicka, Mateusz Ślęczka, Magdalena Greczek-Stachura

Institute of Biology, Pedagogical University of Kraków, Podchorążych 2 St., 30-084 Kraków, Poland, *katarzyna.mozdzen@up.krakow.pl

The photosynthetic activity of *Paramecium bursaria* endosymbiotic algae in varying temperature conditions

Introduction

Microbial organisms are ideal to study adaptation to a variable environment. They are characterised by large population sizes, short generation time, and the ability to manipulate their environment in controlled conditions (Jessup et al., 2004).

Paramecium bursaria Ehrenberg 1831 is cosmopolitan organism, inhabiting standing or slowly flowing water with relatively high purity. *P. bursaria* forms the endosymbiotic relationship with algae of *Chlorella* species (Reisser, 1980). This relationship is an unusual example of optional and mutualist interaction between the two species. There are up to several hundred symbiotic algae inside the cell of *P. bursaria* (Karakashian et al., 1968) (Fig. 1). The symbiotic algae are enclosed in a perialgal vacuole membrane (derived from the host digestive vacuole), and this membrane protects the algae from the hosts lysosomal digestion (Kodama, Fujishima, 2005). The host cell protects endosymbionts from infections by *Chlorella virus*. *Paramecium* supply algal cells with nitrogen components and the CO_2 necessary for photosynthesis (Reisser, 1980; Albers, Wiessner, 1985; Kodama, Fujishima, 2005). Green endosymbionts carry out photosynthesis and thus provide the host with maltose and oxygen (Brown, Nielsen, 1974); therefore, *P. bursaria* becomes completely or partially independent of the external source of food (Sommaruga, Sonntag, 2009).

Endosymbionts inside *P. bursaria* are sensitive to different environmental factors, e.g., temperature. Long-term exposure ciliates to low temperatures may cause changes in the early stages of development of their metabolism and consequently lead to the microorganisms extinction (unpublished). Global warming leads to changes in the process of photosynthesis and respiration in autotrophic organisms. PSII seems to be one of the most thermo-sensitive protein complex pigments, which regulates photosynthetic activity in algae, cyanobacteria, as well as in higher plants (Strasser et al.,

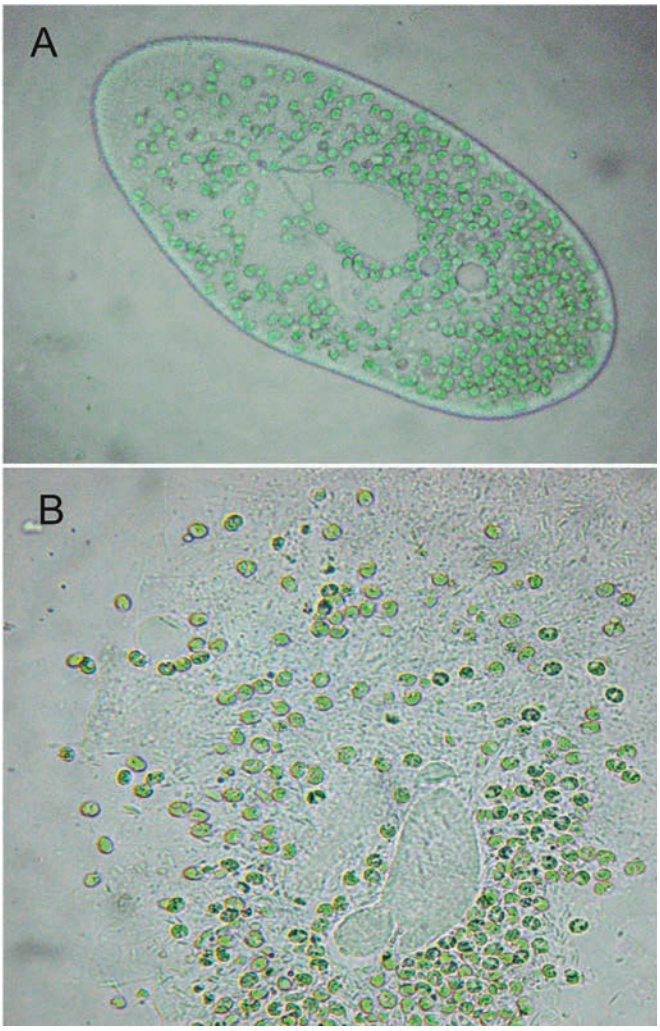

Fig. 1. *Paramecium bursaria* with green endosymbionts – A; endosymbiotic algae isolated from the *Paramecium bursaria* cell – B (Photo. M. Ślęczka)

1995; Morgan-Kiss et al., 2006). *Chlorella vulgaris* Beijer. cells regulate photosynthetic processes at the level of LHCII polypeptides, chlorophyll molecules, as well as through the xanthophyll cycle, in response to different temperatures and light intensities (Wilson, Huner, 2000).

The aim of this study was to investigate the effects of temperatures (21°C, 24°C, 27°C, 30°C, and 33°C) on the photosynthesis carried out by endosymbiotic green algae of two *P. bursaria* strains from warm climate (Ardmore, USA) with an average annual temperature of +23.7°C (Ard7) and from cold climate (Kamchatka, Russia) with an average air temperature of -6°C (KD64).

Material and methods

The experiments were conducted at the Institute of Biology of Pedagogical University of Kraków. The study material was *Paramecium bursaria* strains from (1) Kamchatka (KD64) located in the Asian part of Russia (58°36′40″N; 38°54′44″E) and (2) Ardmore (Ard7) located in the south-eastern Carter County, Oklahoma, United States (34°10′52″N; 97°07′46″W).

Paramecium bursaria culture techniques

Green *Paramecium bursaria* strains were grown on a lettuce medium with *Klebsiella pneumoniae* (SMC strain) (Sonneborn, 1970). The cultures were maintained under constant light/dark cycle (12L:12D) at 18°C, at light intensity 200 μmol m^{-2} s^{-1} for 7 days at the following temperatures: 21°C, 24°C, 27°C, 30°C and 33°C.

Chlorophyll *a* fluorescence

Chlorophyll *a* fluorescence was measured using a Handy Plant Efficiency Analyser fluorimeter (Hansatech Instruments, United Kingdom). A 1 ml sample, with green *P. bursaria*, was taken into glass cell, then the sample was darkened for 5 minutes

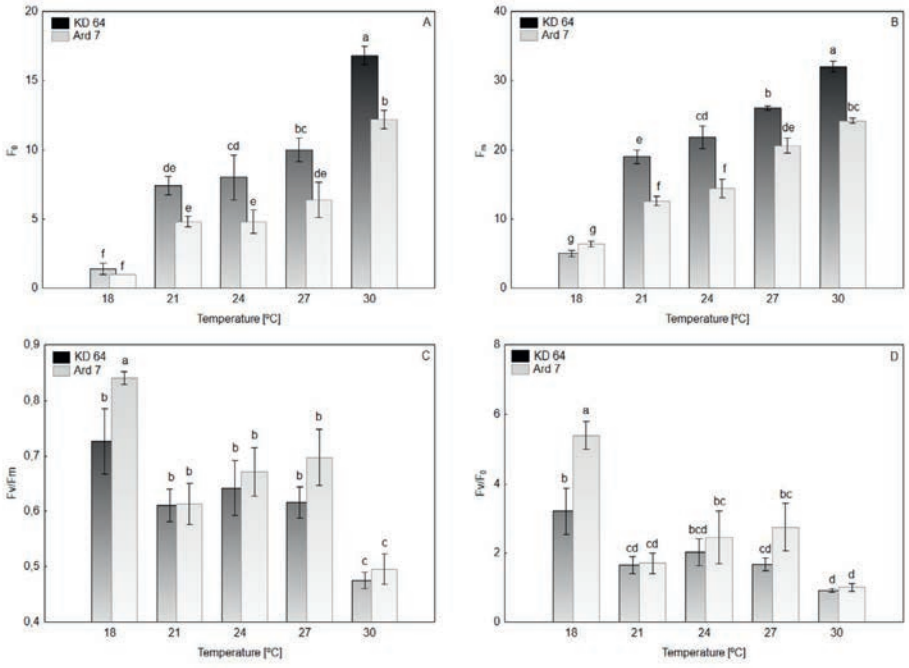

Fig. 2. Chlorophyll *a* fluorescence parameters of *Paramecium bursaria* strains: KD64 and Ard7, incubated at different temperatures; different letters differ significantly according to the Duncan test at $p \leq 0.05$; n = 5

to make the conditions needed to expire the light phase of photosynthesis. The obtained results were analysed as follows: F_0 – chlorophyll fluorescence intensity measured when all photosystem II reaction centres are open, F_m – maximal chlorophyll fluorescence intensity measured when all photosystem II reaction centres are closed, F_v – variable chlorophyll fluorescence (F_m/F_0), F_v/F_0 – efficiency of the water-splitting complex on the donor side of PSII and F_v/F_m – maximum quantum yield of PSII. In addition, T_{fm} – time needed for reaching F_m (ms), RC/ABS – index expression as the density of reaction centres (RC), PI – indicator of the functioning of PSII, TRo/RC – trapped energy flux per cross section (RC) at t = 0, ETo/RC – electron transport flux per cross section (RC) at t = 0, and Vj – relative change in chlorophyll fluorescence during the light phase of photosynthesis.

Emission fluorescence – spectrofluorimetry method

Measurement of blue-green and red fluorescence emission spectra were performed according to Lichtenthaler et al. (2004) with a spectrofluorimeter (Perkin-Elmer LS55B, United Kingdom) equipped with a liquid measuring device. Measurements of fluorescence intensity in the range of blue-green light (430–650 nm) were performed at 390 nm and near and far red (650–800 nm) with blue 430 nm. The slot for the excitation radius was 15 nm, and for the emitted 20 nm. Results were analysed using FL WinLab version No. 3.00.

Statistic analysis

A parametric multi-factorial ANOVA / MANOVA test was used to compare the variables tested, based on multiple Duncan homogeneous tests at $p \leq 0.05$; n = 5. Calculations were made using StatSoft, Inc. (2014). STATISTICA®12. Program.

Results

The minimum (F_0) and maximum (F_m) fluorescence values for both strains increased with temperature. The highest F_0 values were observed at 30°C. Parameters of maximum PSII (F_v/F_m) photochemical efficiency and maximum splash water yield after PSII donor side (F_v/F_0) were highest at 18°C and lowest at 30°C for two *Paramecium bursaria* strains (Fig. 2).

The chlorophyll *a* fluorescence values were considerably different at tested temperatures compared to the control group. The chlorophyll fluorescence parameters (F_0 and F_m) were significantly higher for the KD64 strain compared to the Ard7 strain (Fig. 2–3).

The blue-green and red fluorescence emission spectra in KD64 and Ard7 strains were similar in the shape (Fig. 4). The increase of blue-green emission fluorescence

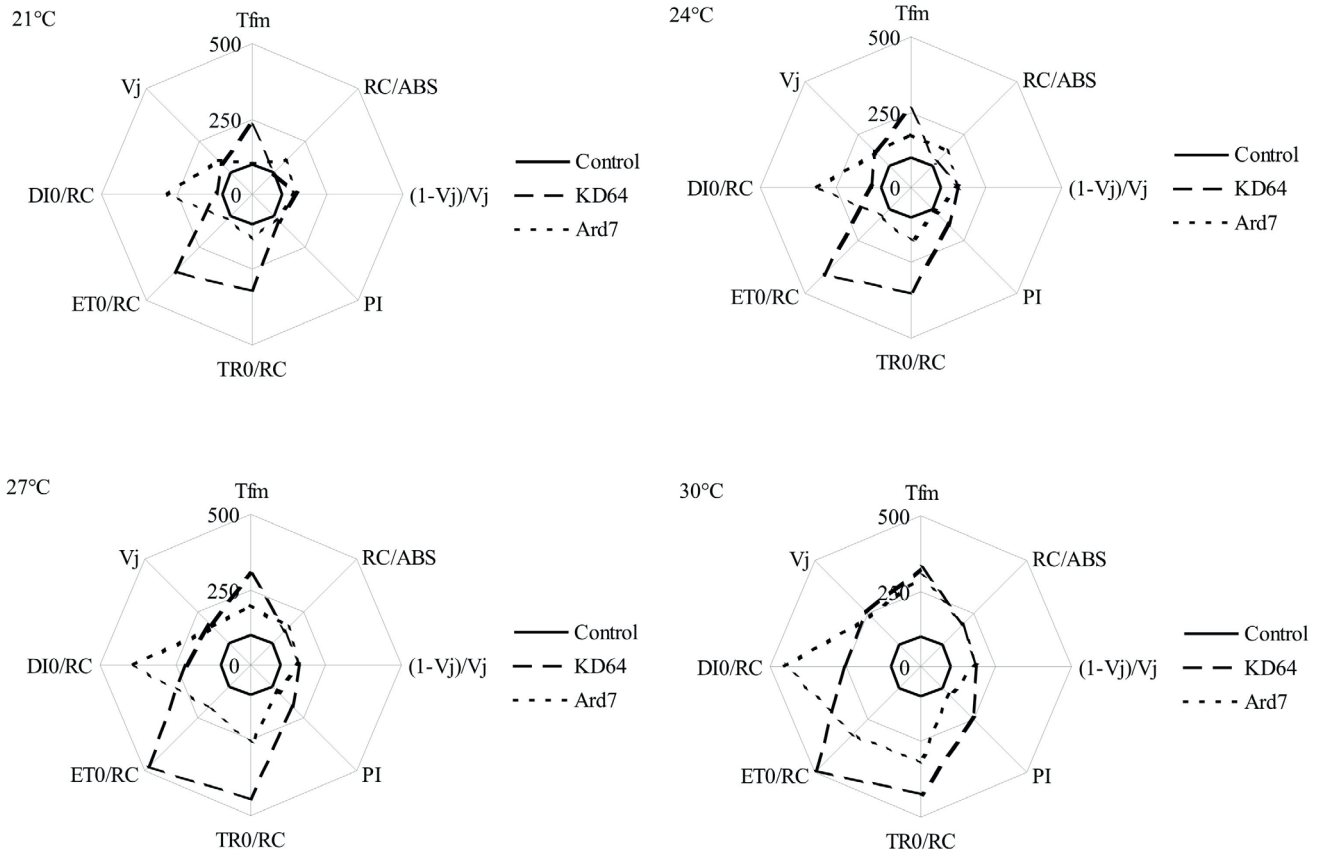

Fig. 3. Chlorophyll *a* fluorescence parameters [shown as % of control] of *Paramecium bursaria* strains incubated at different temperatures

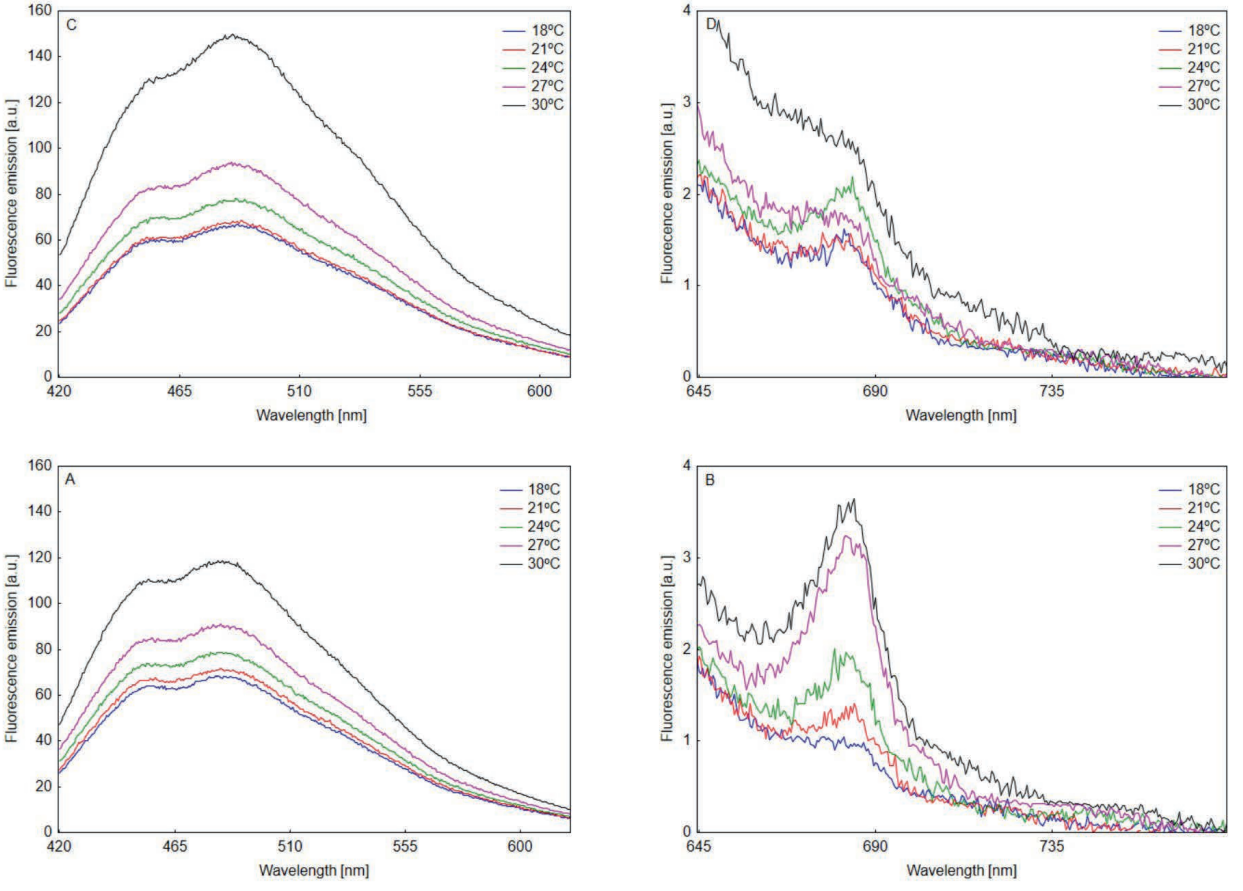

Fig. 4. The blue-green (A) and red (B) fluorescence emission spectra KD64 and Ard7 strains of *Paramecium bursaria* incubated at different temperatures

was clearly shown at two wavelengths. The first peak was observed at a wavelength 450–460 nm, and the second peak was at 485–490 nm. The blue-green fluorescence emissions at 21°C were similar to the control group. The fluorescence emission increased with temperature.

Red fluorescence emission spectra for both strains of *P. bursaria* were characterised by a distinct peak at a wavelength 675–685 nm with an arm at 750 nm. Fluorescence intensity increased at temperatures 24°C to 30°C.

The values of F450/F685, F450/F735, F485/F685, and F485/F735 for *P. bursaria* strains decreased with increasing temperature. The parameter F450/F530 increased with temperature, and the highest value was observed at 30°C (Tab. 1).

Tab. 1. Fluorescence emission factors values of Ard7 – (A) and KD64 – (B) strains incubated at different temperatures. Values shown as different letters within the line differ significantly according to the Duncan test at $p \leq 0.05$; $n = 5$

Ratio	Temperature [°C]									
	18		21		24		27		30	
	A	B	A	B	A	B	A	B	A	B
F450/F685	65.5^{a}	49.1^{b}	48.5^{b}	45.9^{bc}	40.9^{bcd}	42.7^{bcd}	36.90^{cd}	44.2^{bcd}	26.9^{e}	35.2^{d}
F450/F735	652.7^{a}	341.9^{ab}	392.0^{ab}	339.5^{ab}	373.3^{ab}	299.2^{ab}	298.5^{ab}	292.9^{ab}	278.1^{b}	262.6^{b}
F450/F530	1.43^{c}	1.10^{g}	1.46^{bc}	1.27^{f}	1.47^{b}	1.27^{f}	1.47^{b}	1.30^{e}	1.72^{a}	1.40^{d}
F485/F685	72.3^{a}	52.9^{bc}	52.6^{bc}	56.1^{b}	44.6^{cd}	49.3^{bcd}	44.0^{cd}	48.3^{bcd}	29.2^{e}	40.2^{d}
F485/F735	724.2^{a}	394.0^{ab}	466.3^{ab}	391.6^{ab}	407.6^{ab}	341.1^{ab}	323.5^{ab}	320.6^{ab}	301.0^{b}	300.2^{b}
F685/F735	6.1^{a}	5.4^{a}	9.2^{a}	6.6^{a}	9.8^{a}	8.0^{a}	10.5^{a}	7.4^{a}	10.6^{a}	8.5^{a}

Discussion

Temperature has a major structuring effect at all levels of biological organisation. At the cell level, the temperature affects both energetic requirements and division rates, growth rate, and the decomposition and exchange of carbon dioxide and oxygen. The functioning of the whole ecosystems depends on temperature (Brown et al., 2004; Savage et al., 2004).

Green algae tolerance is not the same for constant and variable temperature treatments (Feder, Hofmann, 1999). Ciliates respond promptly and differently to environmental change (Jiang, Morin, 2004; Esteban, Finlay, 2007). In the present study, there was revealed a significant effect of temperature on the photosynthetic activity of endosymbionts inside the *Paramecium bursaria* cells, which originated from a warm and cold climate. One-week incubation of ciliates at different temperatures caused changes in chlorophyll *a* fluorescence parameters (Fig. 2–3), and an increase of fluorescence

emission intensity (Fig. 4). The values of emission fluorescence ratios (F450/F530 and F685/F730) were increased with temperature (Tab. 1). These changes may indicate a decrease in the efficiency of primary reactions occurring in PSII and the activation of defence mechanisms of endosymbiont photosynthetic apparatus (Lichtenthaler, Rinderle, 1988; Chemeris et al., 2004). At high temperatures, cell membrane permeability and damage of PSII subunits increase (Kota et al., 2002). The changes are observed (I) in the structure of proteins and lipids, (II) in the functioning of ion channels, (III) disturbances in electron transport and in the reduction of electron acceptors, (IV) in the efficiency of oxygen extraction, and (V) the dissipation of heat (Weng, Lai, 2005). High temperatures cause a blockade of energy transfer from the reaction centre to plastochinone (Reigosa, Weiss, 2001). Changes in F450/F530 values indicate an increase in phenolic compounds, and changes in F685/F730 values indicate a decrease in chlorophyll content (Lang et al., 1991; Lichtenthaler et al., 2004).

The rate of *P. bursaria* metabolism depends on the number of endosymbiotic *Chlorella* cells and their photosynthetic activity (Weis, 1969). The photosynthetic products of symbiotic green algae increase the tolerance to high temperatures of the host cell (Iwatsuki et al., 1998). *P. bursaria* cells with *Chlorella* algae are more tolerant to high temperatures than algae-free ciliates (Miwa, 2009).

The studies on the effect of temperature on the morphology and physiology of algae show that the optimal growth temperatures for *Chlorella vulgaris* range from 26°C to 34°C (Mayo, 1997; Ma et al., 2014). Duncan et al. (2011) showed that *Paramecium* from variable environments grow well at both 23°C and 35°C. At temperatures from 29°C to 39°C, *Chlorella* sp. strain R-06/2 originating from geothermal source in Rupite (Bulgaria) is highly photosynthetically efficient (Gacheva, Pilarski, 2008). Under natural lighting conditions, the highest increase in chlorophyll content, carotenoids and proteins in *C. vulgaris* are observed at temperatures from 25°C to 30°C. Under continuous light conditions and at temperatures from 30°C to 35°C, algae growth is minimal (Sharma et al., 2012). Changes in physiological properties are due to the endosymbiotic close relationship between paramecium and algae (Reisser, 1986). According to McAuley et al. (1996), the host regulates the growth of symbiotic algae. In the present study, the higher differences in photosynthetic activity were observed in the KD64 strain from Kamchatka (Fig. 2–4; Tab. 1).

The environmental stressors may cause many adverse changes in aquatic ecosystems, as well as for the economy and human health. That is why it attaches great importance to ensuring continuous monitoring of waters, so that changes can be noted and appropriate corrective or preventive measures taken in the natural environment. Given the significant ecological role played by ciliates, it is important to understand how temperature affects the adaptation of organisms in their local environment.

Conclusion

The study showed a significant effect of temperature on the activity of the photosynthetic apparatus of the *Paramecium bursaria* green endosymbionts. With an increase of temperature, changes in PSII were observed. High temperature caused an increase of blue-green and red fluorescence emission of endosymbiotic algae. The strain of *P. bursaria* from Kamchatka (KD64) was more sensitive than the strain from Admore (Ard7).

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Abstract

The aim of this study was to investigate the effect of higher temperatures on the photosynthesis of endosymbiotic *Chlorella* sp. of two *Paramecium bursaria* Ehrenberg 1831 strains originating from regions with a warmer and colder climate (Ardmore – USA and Kamchatka – Russia, respectively). After seven days of protozoa incubation at 18°C (control), 21°C, 24°C, 27°C, 30°C and 33°C, the chlorophyll *a* fluorescence measurements were carried out and fluorescence spectra were measured in blue-green and red light. As a result of the studies, a significant effect of higher temperature on the photosynthesis process of *P. bursaria* endosymbionts was observed. Weekly incubation at 33°C was lethal for both protozoan strains in comparison to the control temperature (18°C). The blue-green fluorescence spectra were characterised by marked peaks at 450 nm and 490 nm. Within the red light range, the peak was observed at about 690 nm with a lesser arm at 730 nm. Endosymbionts from Kamchatka were more sensitive to the temperature increase than algae from areas with relatively warm climates.

Key words: emission fluorescence, high temperatures, PSII activity, spectrofluorimetry, *Chlorella vulgaris*

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Aktywność fotosyntetyczna endosymbiotycznych glonów *Paramecium bursaria* w zróżnicowanych warunkach temperatury

Streszczenie

Celem niniejszej pracy było zbadanie wpływu podwyższonej temperatury na przebieg procesu fotosyntezy endosymbiontów z gatunku *Chlorella* sp. dwóch szczepów *Paramecium bursaria* Ehrenberg 1831, pochodzących z terenów o niskich i wysokich temperaturach powietrza (Ardmore – USA i Kamczatka – Rosja). Po 7 dniach inkubacji pierwotniaków w każdej z temperatur 18°C (kontola), 21°C, 24°C, 27°C, 30°C i 33°C przeprowadzono pomiary fluorescencji chlorofilu *a* i wyznaczono widma emisji fluorescencji w zakresie niebiesko-zielonym i czerwonym.W wyniku przeprowadzonych badań zaobserwowano istotny wpływ podwyższonej temperatury na proces fotosyntezy endosymbiontów *P. bursaria*. Tygodniowa inkubacja w temperaturze 33°C była letalna dla obu szczepów pierwotniaka, w porównaniu z temperaturą kontrolną (18°C). Widma emisji fluorescencji niebiesko-zielonej charakteryzowały wyraźnymi pikami przy 450nm i 490 nm. W zakresie czerwonym pik zaobserwowano przy około 690 nm z mało wyraźnym ramieniem przy 730 nm. Endosymbionty szczepu pochodzącego z Kamczatki były bardziej wrażliwe na wzrost temperatury od glonów pochodzących z terenów o stosunkowo ciepłym klimacie.

Słowa kluczowe: wysoka temperatura, aktywność PSII, spektrofluorymetria, szczepy *Chlorella vulgaris*

Information on the authors

Katarzyna Możdżeń
Her scientific interests concentrate on the effects of different environmental factors (light, ozone, heavy metals, allelopathic extracts) on the morphology and physiology plants cultivated, protected, and invasive species.

Patrycja Zagata Leśnicka
She is graduate of Doctoral Studies at the Institute of Biology at the Pedagogical University in Kraków. Her scientific interests concern microbiology and algology, and especially the endosymbionts of *Paramecium bursaria*.

Mateusz Ślęczka
He graduated from the Environmental Protection at the Pedagogical University in Kraków. His scientific interests concern environmental microbiology.

Magdalena Greczek-Stachura
She is associate professor at the Pedagogical University in Cracow. Her interest is in the broadly understood microbiology and algology. In recent years, her research has focused on endosymbiosis in a group of *Ciliata* (animal Protista).