Night LED illumination in the temperate regions as a model of polar day for algal cultivation in field-installed photobioreactors: Comparison of Svalbard and Central Europe

Jana Kvíderová^{1,2,3*}, Jaromír Lukavský¹

¹Institute of Botany, Academy of Sciences of the Czech Republic, Dukelská 135, Třeboň, Czech Republic ²University of South Bohemia in České Budějovice, Na Zlaté stoce 3, České Budějovice, Czech Republic ³University of West Bohemia, Klatovská 51, Plzeň, Czech Republic

Abstract

The low-temperature algal biotechnology starts to develop in the Polar Regions, and especially in the Arctic. Light is crucial environmental factor in algal mass cultivation, therefore knowledge of the light environment and its modeling is crucial for design of the photobioreactors. The light conditions in three different environments were compared: natural diel light cycle during the polar summer (June-August) in Syalbard and in winter/spring (January – March) in the Central Europe outdoor and in the greenhouse photobioreactor, and in greenhouse photobioreactor equipped by additional night LED illumination in central Europe in winter/spring. In Svalbard, the monthly mean diel PAR values ranger from 126 to 395 μ mol m⁻² s⁻¹, and the monthly diel sums of the PAR ranged from 2.38 to 7.47 MJ m⁻² d⁻¹. In the Central Europe in natural diel light cycle, the monthly mean diel PAR values and monthly diel sums of the PAR were generally lower, 57 - 248 μ mol m⁻² s⁻¹ and 1.08 and 4.69 MJ m⁻² d⁻¹ in outdoor and 26 – 107 μ mol m⁻² s⁻¹ and 0.50 - 2.03 69 MJ m⁻² d⁻¹ in the sun-illuminated photobioreactor. When additional night LED illumination, lasting from 12 to 14.7 hrs and from 12 to 15.3 hrs in 2021 and 2022, respectively, was provided, the monthly mean diel PAR values and monthly diel sums of the PAR increased to 479 - 598 umol m⁻² s⁻¹ and 9.06 - 11.31 MJ m⁻² d⁻¹, respectively. Since the Svalbard maxima of diel sum of PAR are comparable to the values found in the night LED illuminated greenhouse photobioreactor, the night LED illumination in winter/spring in Central Europe should be proposed for model cultivations in the Polar Region in summer.

Key words: low-temperature algal biotechnology, Svalbard, Central Europe, light conditions, PAR

DOI: 10.5817/CPR2023-1-6

Received March 22, 2023, accepted June 7, 2023.

^{*}Corresponding author: J. Kvíderová <jana.kviderova@objektivem.net>

Acknowledgements: The work was supported by projects Technology Agency of the Czech Republic (TN 01000048), institutional long-term research plan of the Czech Academy of Sciences (RVO67985939), the Ministry of Education, Youth and Sports of the Czech Republic (LTAIN 19139) and by the Czech Science Foundation (project 22-08680L).

Introduction

During polar day, i.e. continuous daylight in the Polar Regions during local summer, the continual light availability could be exploited in algal biotechnology. The algal biotechnology starts to develop as the human presence in the Polar Regions, and especially in the Arctic, increases due to climate changes in these regions. The algal biotechnological applications may help to minimize the impact of human activities on pristine polar ecosystems and to develop novel low-temperature algal technologies suitable for polar environments (Kvíderová et al. 2017). These applications could be also used during the cold part of the year in the temperate regions since the cultivation of standard mesophilic strains is limited temporarily from May to September. The low-temperature applications could extend the cultivation period to whole year and allow maximum efficiency in the cultivation units utilization.

The ideal strain for low-temperature biotechnological applications should be able to grow well at low temperatures, but also it should tolerate short-term exposure in range of hours to temperatures even above 25°C (Kvíderová et al. 2017). To identify such strains is relatively difficult because, due to biodiversity protection, only local strains should be used in the Polar Region and/or in the temperate zone. Since the growth optima of strains isolated from similar low temperature conditions may differ (Shukla et al. 2020) as well as their requirements for nutrients (Shukla et al. 2011), extended testing of growth optima and limits is necessary as initial part of bioprospection, reducing thus further the number of suitable algal strains fulfilling all, or at least the majority of criteria mentioned above. During our studies, we identified several strains suitable for low-temperature applications. These strains include *e.g. Edaphochlorella mirabilis* (Shukla et al. 2013) *Bracteacoccus bullatus* (Lukav-ský et al. 2023) or *Dictyosphaerium chlorelloides* (Kumar et al. 2017).

In the mass cultivations, photosynthetically active radiation (PAR) is usually the most limiting environmental factor (Pulz and Scheibenbogen 1998, Sforza et al. 2012). The respiration losses during the night phase may reach even 5 - 8 % of biomass content (Edmundson and Huesemann 2015). The problem of the light limitation should be avoided by additional illumination which should be relatively expensive (Abomohra et al. 2019, Blanken et al. 2013). From the point of light limitation, the polar summer should be ideal for algal cultivation since the input of the light energy from the Sun seems to be inexhaustible. However, the light conditions in the Polar Regions may be very variable and should be site-specific. The data on PAR radiation are scare, and results are often based on recalculations from global radiation data (for instance, Addison and Bliss 1980, Courtin and Labine 1977. Friedmann et al. 1987. Henry et al. 1994, Hodson et al. 1998, Komárek and Elster 2008, Krezel and Pecherzewski 1981, Labine 1994, Láska et al. 2012, McKay et al. 1993, Tenhunen et al. 1992, recalculated to PAR in Kvíderová et al. 2017).

The aim of this work was to analyze the light conditions, PAR dial courses in particular, typical for polar summer in Longyearbyen, Svalbard, and cold part of the year (winter period) in the temperate zone (Třeboň, Czech Republic). Additionally, the effect of additional continuous night LED illumination in the temperate zone (Třeboň, Czech Republic) was evaluated and considered as possible model conditions of the polar summer.

Material and Methods

PAR data collection

The data were collected by QTie datalogger (EMS Brno, CZ) in 10 min. or 15 min. intervals during the summer seasons in the Polar Regions (N 78° E 16°, Longvearbyen, Svalbard) and during nonsummer seasons in the temperate regions (N 49° E 15°, Třeboň, Czech Republic). The dataloggers were positioned only outdoor in Svalbard. In Třeboň, they were positioned outdoor as well as inside the greenhouses where the experimental large-scale thin-layer photobioractors (150 L) were located. The large-scale cultivation was performed in the thin-layer photobioreactors of volume of 150 L and area of 12 m^2 (Doucha and Lívanský 1996; used recently by Řezanka et al. 2017 and Lukavský et al. 2023). One photobioreactor was exposed

to natural diel light regime and the second one was equipped by 25 pieces of OptimaLED 134W LED panels (Thome Lightning, CZ) to illuminate the photobioreactor during night. The LED panels are suspended above the photobioreactor in two rows in distance of 0.5 m from the plates (Fig. 1). During a day, this second photobioreactor was also exposed to natural diel light regime. The exact days of data collections are summarized in Table 1.

Only the data from complete days (24 hrs) were included in analyses. The "night" in natural diel light cycle was defined as interval from sunset +30 min. to sunrise -30 min. according to visual flight rules.



Fig. 1. The night LED illumination of the large-volume (150 L) thin-layer photobioreactor at the Institute of Botany CAS, Třeboň, Czech Republic.

J. KVÍDEROVÁ & J. LUKAVSKÝ

Light source	Start date	End date	Locality	Reference
Sun (O)	7.8.2016	22.8.2016	Longyearbyen	Svalbard Kvíderová & Elster 2017
Sun (O)	13.8.2017	30.8.2017	Longyearbyen	Svalbard Souquieres et al. 2017
Sun (O)	20.8.2018	31.8.2018	Longyearbyen	Svalbard
Sun (O)	23.6.2022	30.8.2023	Longyearbyen	Svalbard
Sun (G)	8.1.2021	23.2.2021	Třeboň	Czech Republic
Sun (G)	11.1.2022	27.3.2022	Třeboň	Czech Republic
Sun + LED (G)	17.2.2021	24.3.2023	Třeboň	Czech Republic
Sun + LED (G)*	11.1.2022	22.3.2022	Třeboň	Czech Republic
Sun (O)	6.1.2022	29.3.2022	Třeboň	Czech Republic

Table 1. The summary information on analyzed data. The asterisk indicates that only part of the data was presented in given reference. *Abbreviations*: G – greenhouse, O – outdoor. *Note*: *LED were not in operation between February 4 and 6, 2022.

Statistic al analysis

The statistical analyses were performed using Statistica 14.0 software (TIBCO Software, USA).

Results and Discussion

The mean irradiances in Svalbard indicated mean medium light conditions in June and July in natural diel light cycles, and low-light conditions in August. In the Central Europe in winter/early spring, the mean PAR irradiances were comparable, and even lower than in summer in Svalbard, especially in January (Table 2). The observed PAR values were similar to other studies (for instance Addison and Bliss 1980, Courtin and Labine 1977, Friedmann et al. 1987, Henry et al. 1994, Hodson et al. 1998, Komárek and Elster 2008, Krezel and Pecherzewski 1981, Labine 1994, Láska et al. 2012, Lukavský et al. 2023, McKay et al. 1993, Shukla et al. 2013, Tenhunen et al. 1992). However, even in Svalbard in summer and in the Central Europe in winter, the PAR values reached and occasionally exceeded 1000 μ mol m⁻² s⁻¹. The duration of high irradiance periods above 1000 μ mol m⁻² s⁻¹ is usually tens of minutes up to ca 3 hrs, often interrupted by periods of lower irradiances in Svalbard as well as in the Central Europe. The mean PAR values that had exceeded the 1000 μ mol m⁻² s⁻¹ limit, were 1059 and 1096 in Svalbard in 2016 and 2022, and 1124 μ mol m⁻² s⁻¹ in the Central Europe. In Svalbard in 2017 and 2018, no such high PAR values were observed at all, and they were very rare in August in 2016 and 2022. In the Central Europe, such high irradiances occurred in February and March, not in January. The occurrence of high irradiances may be season-specific due to the different Sun elevation above the horizon, and/or it may reflect actual weather conditions.

LIGHT CONDITIONS IN POLAR AND TEMPERATE REGIONS

	n	PAR [umol m ⁻² s ⁻¹]			Diel Σ_{pap} [M.J m ⁻² d ⁻¹]		
		Mean	MIN	MAX	Mean	MIN	MAX
Svalbard 2016 ⁰	1536	171	2 (2-44)	1080 (274-1080)	3.24	1.20	6.04
Svalbard 2017 ⁰	1728	145	0 (0-22)	793 (246-793)	2.74	1.31	4.48
Svalbard 2018 ⁰	1152	126	1 (0-7)	815 (235-815)	2.38	1.22	4.16
Svalbard 2022 ⁰	9936	257	1 (1-146)	1473 (244-1473)	4.85	1.29	11.59
- June	1152	395	12 (12-146)	1473 (620-1473	7.47	2.96	10.45
- July	4464	292	11 (11-119)	1277 (244-1277)	5.52	1.29	11.59
- August	4320	183	1 (1-33)	1023 (243-1023)	3.47	1.47	5.26
Třeboň 2021 Sun ^G	6768	40	0	439 (62-439)	0.75	0.21	1.55
- January	3456	32	0	318 (149-318)	0.61	6.41	0.90
- February	3312	47	0	439 (62-439)	0.89	0.21	1.55
Třeboň 2022 Sun ^G	10944	65	0	1610 (34-1610)	1.22	0.14	3.20
- January	3024	26	0	329 (34-329)	0.50	0.14	0.83
- February	4032	52	0	535 (135-535)	0.99	0.41	1.62
- March	3888	107	0	1610 (182-1610)	2.03	0.73	3.20
Třeboň 2021 LED ^G	5184	505	4 (4-10)	928 (742-928)	9.54	8.29	11.22
- February	1728	557	4 (4-9)	928 (880-928)	10.52	9.71	11.22
- March	3456	479	4 (4-10)	896 (741-896)	9.06	8.29	9.93
Třeboň 2022 LED ^G	<i>9792</i>	561	5 (5-12)	935 (839-935)	10.61	9.35	11.89
- January	3024	598	5 (5-12)	935 (886-935)	11.31	10.79	11.89
- February	3600	555	5 (5-12)	912 (869-912)	10.89	9.98	10.83
- March	3168	533	6 (6-10)	899 (839-899)	10.08	9.35	10.59
Třeboň 2022 Sun ^o	11952	146	0	1556 (75-1559)	2.76	0.32	6.57
- January	3744	57	0	858 (75-858)	1.08	0.32	1.97
- February	4032	122	0	1402 (303-1402)	2.32	0.90	4.09
- March	4176	248	0	1556 (413-1556)	4.69	1.62	6.57

Table 2. The summary characteristics of PAR and the sum of radiation in Svalbard and in Central Europe. *Abbreviations*: n – number of cases, Σ_{PAR} – diel sum of PAR, MIN – minimum, MAX – maximum. The upper index indicates the measuring conditions: G – greenhouse, O – outdoor. The LED and the Sun specifies the light regime of the photobioreator: Sun – only natural diel light regime, LED – combination of the natural diel light regime during the day and additional LED illumination during the night. The values in parentheses indicate range of diel minima and maxima.

Such irradiances could lead to temporal photoinhibition in general (Falkowski and LaRoche 1991, Falkowski and Raven 2007), however even low-light adapted polar algae could tolerate short-term exposition to high irradiances. The xanthophycean alga *Vaucheria* was adapted to relatively low irradiances as the saturation irradiance ranged between 113 and 173 μ mol m⁻² s⁻¹ for standard gasometric light curve meas-

urements and between 208 and 308 µmol $m^{-2} s^{-1}$ for rapid light curve measurements based on variable chlorophyll fluorescence (Kvíderová and Elster 2017, Souquieres et al. 2017, Kvíderová et al. 2019). The differences in the saturation irradiances are caused by differences in limitations of the measured processes, i.e. CO₂ fixation and electron transport in the photosystem II (Hupp et al. 2021). The short-term exposition up to 650 umol m⁻² s⁻¹ for 6 min. during the gasometric and fluorescence measurements did not affect the photosynthetic activity (Kvíderová et al. 2019). The continuous variable chlorophyll measurement based on effective quantum vield protocol did not show any limitation for irradiances up to 700 umol m⁻² s⁻¹ (Kvíderová and Elster 2017, Souquieres et al. 2017, Kvíderová et al. 2019).

The greenhouse roof reduced the incoming PAR by about a half, leading to possible light-limiting conditions in the photobioreactors, especially in dense cultures, in the greenhouses in winter. When additional night illumination provided by the LEDs was added, the mean irradiances rised to $500 - 600 \ \mu\text{mol m}^{-2} \ \text{s}^{-1}$. The slight decrease of the mean values during the shift from winter to spring was probably caused by prolongation of the light period of a day. The period of the LED illumination was shorter, and the irradiance provided only by the Sun was not sufficient to compensate fully the LEDs contribution (Table 2).

In continuous light regime, either during the polar summer or under night LED illumination, the diel PAR minima dropped almost 0 μ mol m⁻² s⁻¹ (Table 1). In Svalbard, such conditions occur mainly on cloudy and foggy days and at the end of polar summer in late August when the night period appears again (Fig. 2). In the photobioreactor with the night LED illumination, these conditions occurred during sundown and sunset when the illumination changes (Fig. 3). These diel minima are lower than the compensation point for photosynthesis in algae and water plants (Falkowski and LaRoche 1991, Falkowski and Raven 2007, Van et al. 1976), causing thus probably biomass loss due to negative carbon gain caused by respiration higher then gross photosynthesis. Additional light source or adjustment of the threshold for triggering the LED light sources above the compensation point may reduce these losses.



Fig. 2. The diel course of monthly mean PAR in Svalbard.



Fig. 3. The diel course of monthly mean PAR in Třeboň, Czech Republic. If not specified otherwise, the measurements were performed in photobioreactors in greenhouses.

When considering the diel sum of the PAR radiation received, the June-July maxima in Svalbard occurring on sunny days were comparable to the photobioreactor light regime with night LED illumination (Table 2). The diel Σ_{PAR} were comparable in August on Svalbard and in outdoor March in the Central Europe. In winter

(January and February) in the Central Europe, the diel Σ_{PAR} were even lower than in in Svalbard (Table 2). The observed shifts during the season correspond to changes in the length of the day.

The diel courses of the PAR reflected the period of the year and the geographic position (Fig. 2 and 3). In Svalbard, the diel maxima and minima decreased significantly from June to late August, and the night period appeared in the end of August. In August, minor shifts in PAR were observed, probably due to reduced numbers of days and measurement periods in 2016 – 2022. Nevertheless, the August PAR values were still comparable among the years (Fig. 2).

In the Central Europe in natural diel light regime, the diel PAR maxima increased continually and the light period prolonged from January to March. In the outdoor measurements, the PAR values were about two times higher than in the photobioreactors. The night LED illumination was constant during the cultivation, the shifts in 2021 could be probably caused by change in position of the datalogger. The midday decrease in the PAR values in the photobioreactor with night LED illumination, most profound in March 2022, was probably caused by shadowing of the datalogger by the LED light source (Fig. 3). The night PAR maxima reaching up to 935 μ mol m⁻² s⁻¹ could be considered as photoinhibiting (Falkowski and LaRoche 1991, Falkowski and Raven 2007), but the algal cells in the photobioreactor were in fact subjected to light oscillation with period of ca 30 s light and 10 s dark due to suspension circulation in the photobioreactor (*e.g.* Perner-Nochta and Posten 2007). Moreover, shelf-shading in the dense culture may provide additional protection (Sommaruga et al. 2009).

So far, no study has compared the light conditions during the polar summer and north-temperate winter, especially with focus on possible algal mass cultivations and their applications in Polar Regions. Our study proved that the light conditions of Polar Regions may be simulated in the winter/spring in the Central Europe using additional night LED illumination. Precise LED illumination regulation based on computer LED control could provide more natural light cycle, similar to the real conditions in the Polar Region. In such case, the diel PAR maxima should be probably shifted to midnight, since the diel minima PAR in Svalbard correspond to diel PAR maxima in the Central Europe in winter.

References

- ABOMOHRA, A. E.-F., SHANG, H., EL-SHEEKH, M., ELADEL, H., EBAID, R., WANG, S. and WANG, Q. (2019): Night illumination using monochromatic light-emitting diodes for enhanced microalgal growth and biodiesel production. *Bioresource Technology*, 288: 121514.
- ADDISON, P. A., BLISS, L. C. (1980): Summer climate, microclimate, and energy budget of a polar semidesert on King Christian Island, N.W.T., Canada. Arctic and Alpine Research, 12(2): 161-170.

BLANKEN, W., CUARESMA, M., WIJFFELS, R. H. and JANSSEN, M. (2013): Cultivation of microalgae on artificial light comes at a cost. *Algal Research*, 2(4): 333-340.

COURTIN, G. M., LABINE, C. L. (1977): Microclimatological studies of the Truelove Lowland. *In:* L. C. Bliss (ed.): Truelove Lowland, Devon Island, Canada: A High Arctic ecosystem. University of Alberta Press, Edmonton, pp. 73–106.

DOUCHA, J., LÍVANSKÝ, K. (1996): The way of outdoor thin-layer cultivation of algae and bluegreen algae and bioreactor for carrying out this method. CZ patent 3266-96, CZ 9966U1.

- EDMUNDSON, S. J., HUESEMANN, M. H. (2015): The dark side of algae cultivation: Characterizing night biomass loss in three photosynthetic algae, *Chlorella sorokiniana*, *Nannochloropsis salina* and *Picochlorum* sp. *Algal Research*, 12: 470-476.
- FALKOWSKI, P., LAROCHE, J. (1991): Acclimation to spectral irradiance in algae. Journal of Phycology, 27: 8-14.

FALKOWSKI, P., RAVEN, J. A. (2007): Aquatic photosynthesis. 484 p.

- FRIEDMANN, E. I., MCKAY, C. P. and NIENOW, J. A. (1987): The cryptoendolithic microbial environment in the Ross Desert of Antarctica: Satellite-transmitted continuous nanoclimate data, 1984 to 1986. *Polar Biology*, 7: 273-287.
- HENRY, G. H. R., SVOBODA, J. and FREEDMAN, B. (1994): Standing crop and net production of nongrazed sedge meadow of a polar desert oasis. *In:* J. Svoboda, B. Freedman (eds.): Ecology of a pola oasis. Alexandra Fiord, Ellesmere Island, Canada. Captus University Publications, Toronto, pp. 85–95.
- HODSON, A. J., GURNELL, A. M., WASHINGTON, R., TRANTER, M., CLARK, M. J. and HAGEN, J. O. (1998): Meteorological and runoff time-series characteristics in a small, high-Arctic glaciated basin, Svalbard. *Hydrological Processes*, 12(3): 509-526.
- HUPP, J., MCCOY, J. I. E., MILLGAN, A. J. and PEERS, G. (2021): Simultaneously measuring carbon uptake capacity and chlorophyll a fluorescence dynamics in algae. Algal Research, 58: 102399.
- KOMÁREK, J., ELSTER, J. (2008): Ecological background of cyanobacterial assemblages of the northern part of James Ross Island, Antarctica. *Polish Polar Research*, 29: 17-32.
- KREZEL, A., PECHERZEWSKI, K. (1981): Preliminary data on total radiation in the region of Arctowski Station (King George Island, South Shetland Islands). *Polish Polar Research*, 2: 47-54.
- KUMAR, D., KVÍDEROVÁ, J., KAŠTÁNEK, P. and LUKAVSKÝ, J. (2017): The green alga Dictyosphaerium chlorelloides biomass and polysaccharides production determined using cultivation in crossed gradients of temperature and light. Engineering in Life Sciences, 17(9): 1030-1038.
- KVÍDEROVÁ, J., ELSTER, J. (2017): Photosynthetic activity of Arctic Vaucheria (Xanthophyceae) measured in microcosmos. Czech Polar Reports, 7(1): 52-61.
- KVÍDEROVÁ, J., SHUKLA, S. P., PUSHPARAJ, B. and ELSTER, J. (2017): Perspectives of lowtemperature biomass production of polar microalgae and biotechnology expansion into high latitudes. *In:* R. Margesin (ed.): Psychrophiles: From Biodiversity to Biotechnology. Springer, Cham, pp. 585–600.
- Kvíderová, J., Souquieres, C.-E. and Elster, J. (2019): Ecophysiology of photosynthesis of *Vaucheria* sp. mats in a Svalbard tidal flat. *Polar Science*, 21: 172-185.
- LABINE, C. L. (1994): Meteorology and climatology of the Alexandra Fiord lowland. *In:* J. Svoboda, B. Freedman (eds.): Ecology of a polar oasis. Alexandra Fiord, Ellesmere Island, Canada. Captus University Publications, Toronto, pp. 23–39.
- LÁSKA, K., WITOSZOVÁ, D. and PROŠEK, P. (2012): Weather pattern of the coastal zone of Petuniabukta, central Spitzbergen in the period 2008–2010. *Polish Polar Research*, 33(4): 297-318.
- LUKAVSKÝ, J., KOPECKÝ, J., KUBÁČ, D., KVÍDEROVÁ, J., PROCHÁZKOVÁ, L. and ŘEZANKA, T. (2023): The alga *Bracteacoccus bullatus* (Chlorophyceae) isolated from snow, as a source of oil comprising essential unsaturated fatty acids and carotenoids. *Journal of Applied Phycology*, 35(2): 649-660.
- MCKAY, C. P., NIENOW, J. A., MEYER, M. A. and FRIEDMANN, E. I. (1993): Continuous nanoclimate data (1985-1988) from the Ross Desert (McMurdo Dry Valleys) cryptoendolithic microbial ecosystem. *In:* D. H. Bromwich, C. R. Stearns (eds.): Antarctic meteorology and climatology: Studies based on automatic weather stations. American Geophysical Union, Washington, D.C., pp. 201–207.
- PERNER-NOCHTA, I., POSTEN, C. (2007): Simulations of light intensity variation in photobioreactors. Journal of Biotechnology, 131(3): 276-285.

J. KVÍDEROVÁ & J. LUKAVSKÝ

- PULZ, O., SCHEIBENBOGEN, K. (1998): Photobioreactors: Design and performance with respect to light energy input. *In*: T. Scheper (ed.): Bioprocess and Algae Reactor Technology, Apoptosis. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 123–152.
- ŘEZANKA, T., NEDBALOVÁ, L., LUKAVSKÝ, J., STŘÍŽEK, A. and SIGLER, K. (2017): Pilot cultivation of the green alga *Monoraphidium* sp. producing a high content of polyunsaturated fatty acids in a low-temperature environment. *Algal Research*, 22: 160-165.
- SFORZA, E., SIMIONATO, D., GIACOMETTI, G. M., BERTUCCO, A. and MOROSINOTTO, T. (2012): Adjusted light and dark cycles can optimize photosynthetic efficiency in algae growing in photobioreactors. *PLoS ONE*, 7(6): e38975.
- SHUKLA, S. P., KVÍDEROVÁ, J. and ELSTER, J. (2011): Nutrient requirements of polar *Chlorella*-like species. *Czech Polar Reports*, 1: 1-10.
- SHUKLA, S. P., KVÍDEROVÁ, J., TŘÍSKA, J. and ELSTER, J. (2013): *Chlorella mirabilis* as a potential species for biomass production in low-temperature environment. *Frontiers in Microbiology*, 4: 97.
- SHUKLA, S. P., KVÍDEROVÁ, J., ADAMEC, L. and ELSTER, J. (2020): Ecophysiological features of polar soil unicellular microalgae. *Journal of Phycology*, 56(2): 481-495.
- SOMMARUGA, R., CHEN, Y. and LIU, Z. (2009): Multiple strategies of bloom-forming *Microcystis* to minimize damage by solar ultraviolet radiation in surface waters. *Microbial Ecology*, 57(4): 667-674.
- SOUQUIERES, C.-E., KVÍDEROVÁ, J. and ELSTER, J. (2017): *Vaucheria* sp. a xanthophycean alga from Svalbard intertidal zone. Year 2. *Czech Polar Reports*, 7(2): 323-326.
- TENHUNEN, J. D., LANGE, O. L., HAHN, S., SIEGWOLF, R. and OBERBAUER, S. F. (1992): The ecosystem role of poikilohydric tundra plants. *In:* F. S. I. Chapin, R. L. Jefferies, J. F. Reynolds, G. R. Shaver, J. Svoboda (eds.): Arctic ecosystem in a changing climate. An ecological perspective. Academic Press, San Diego, pp. 213–237.
- VAN, T. K., HALLER, W. T. and BOWES, G. (1976): Comparison of the photosynthetic characteristics of three submersed aquatic plants. *Plant Physiology*, 58(6): 761-768.