Photosynthesis ecophysiology of polar *Vaucheria* sp. – inter-annual comparison

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Abstract

The *Vaucheria* sp. microbial mats represent the most important primary producer in the tidal flat in Adventdalen, Svalbard. Its photosynthetic activity was monitored *ex situ* in a microcosm in late Arctic summer in 2016 and 2017 using variable chlorophyll fluorescence measurements with blue and red excitation lights. The effective quantum yield (Φ_{PSII}) was measured, and the photosynthetic relative electron transport rate (rETR) was calculated. During the measurement period, the microclimate data, air temperature and photosynthetically active radiation (PAR), were recorded as well. Year 2016 was slightly warmer than year 2017. Despite of higher maximum PAR values found in 2016, the mean irradiance reached higher values in 2017 than 2016. When using red light excitation, the rETR and effective quantum yield values were lower than those measured using blue excitation light in 2016. However, opposite results were recorded in 2017, indicating thus rather sample-specific differences. According to redundancy analysis, the PAR was confirmed as the main driver of photosynthesis in late Arctic summer in both years. No serious photoinhibition, expressed as serious systematic decline of the rETR, was observed in both years indicating rapid photoacclimation of *Vaucheria* sp. photosynthesis to changing light environment. The air temperature was found to be less important driver of the photosynthetic activity. The inter-annual comparisons showed increased photosynthetic activity in 2017, probably caused by higher PAR in 2017, by differences in microcosmos design and/or heterogeneity of samples.

Key words: Svalbard, variable chlorophyll fluorescence, photosynthesis drivers

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Introduction

At present, the Arctic coastline ecosystems, located at the land-ocean interface, are being subjected to changes caused by the rise of sea level and increasing environmental and anthropogenic pressures ([1] - ACIA 2005). The coastal ecosystems within the tidal zone in vicinity of river estuary are characterized by rapid changes. They are, however, only partly predictable due to combination of diurnal cycles of temperature, irradiance and tidal cycles resulting in different combinations of temperature, irradiance, salinity and water availability (Szymelfenig et al. 1995). Therefore, such ecosystems could be considered as poikiloenvironment (Gorbushina and Krumbein 1999) or marginal type of extreme environment (Elster 1999). Survival of autotrophs in such dynamic environment requires a high degree of tolerance to broad ranges of environmental conditions and their ability of rapid acclimation to changing environment (Elster 1999). Several studies have been performed in the Svalbard to assess coastal ecosystem dynamics, biological diversity and ecophysiological properties of autochthonous (micro)organisms (Kvíderová and Elster 2017, Kvíderová et al. 2019, Souquieres 2018, Szymelfenig et al. 1995, Weslawski et al. 1993, Weslawski and Szymelfenig 1999). Our study focuses on the changes in photosynthetic activity in a tidal alga as dependent on season, and microclimatic characteristics (photosynthetically active radiation - PAR, and temperature).

The benthic communities in estuarine tidal flats contribute significantly to the total ecosystem productivity of the ecosystem, to nutrient cycling and to sediment stabilization ([1]-ACIA 2005, Bellinger et al. 2009, Sundbäck et al. 2000). In case of the Adventdalen tidal flat, microbial mats of *Vaucheria* sp. (Xanthophyceae) are considered the main primary producer (Kvíderová and Elster 2017, Kvíderová et al. 2019, Souquieres 2018). When exposed to the atmospheric air, the algal thalli form conspicuous spike-like structures, mis-described originally by Wiktor et al. (2016) as *Gyrosigma eximium*. The *in situ* photosynthetic activity measurements using variable chlorophyll fluorescence proved good photoacclimation of *Vaucheria* sp. but the main driver(s) of photosynthetic activity in the field remained unidentified (Kvíderová et al. 2019, Souquieres 2018).

Since the long-term monitoring of the photosynthetic activity in the field was not possible, the community and *Vaucheria* sp. thalli were transferred into a microcosm. The microcosm was a plastic box translucent for visible and UV radiation equipped by a pair of monitoring fluorometers recording the effective quantum yield and external temperature/photosynthetically active radiation dataloggers (Kvíderová and Elster 2017, Kvíderová et al. 2019). In the 2016, intact community including sediment layer was submerged in seawater of depth of ca 5 cm, and in addition, the oxygen concentrations were recorded continually near the water surface, in close vicinity the *Vaucherina* sp. thalli and in the sediment (Kvíderová and Elster 2017). Contrary in 2017, pure *Vaucheria* sp. thalli were positioned in open chambers used for gasometric CO_2 consumption/production measurements and were kept wet by submerging the bottom of the chamber into thin layer of filtered seawater (Kvíderová et al. 2019). Since the measurements in microcosmos in 2016 and 2017 overlapped in a period between August 12 and August 23, these datasets were used for inter-annual comparison and determination of the main drivers of photosynthetic activity of the species.

Material and Methods

Experimental site

The measurements were performed at the Czech Arctic Research Infrastructure "Josef Svoboda Station" located in Longyearbyen (78.22331°N, 15.65939°E), Svalbard, between August 12 and 23 in 2016 and 2017. The tidal flat is located approximatelly 200 m from the base. The environmental characteristics of the tidal flat were summarized in Kvíderová et al. (2019) and Souquieres (2018).

Material

Vaucheria sp. thalli were collected in the Adventdalen tidal flat (78.13355°N, 15.4007°E) and transported to microcosm. In the 2016, entire community including the sediment and seawater was enclosed in the microcosmos (Kvíderová and Elster 2017). In 2017, washed *Vaucheria* sp. thalli were positioned in chambers for gasometric CO_2 consumption/production measurements and were kept wet by submerging into a thin layer of seawater (Kvíderová et al. 2019). The experimental setups for both years are described in detail in Kvíderová and Elster (2017), Kvíderová et al. (2019), and Souquieres (2018), respecttively.

Microclimate

The photosynthetically active radiation (PAR) and air temperature (T_{air}) were measured by Minikin QT datalogger (EMS Brno, Czech Republic) in 15 min. interval. The datalogger was positioned in close vicinity (less than 0.5 m) of the microcosm containing the *Vaucheria* sp. biomass.

Photosynthetic activity

The photosynthetic activity, expressed as the effective quantum yield (Φ_{PSII}) was measured using Monitoring Pen MP 100-E portable fluorometers (Photon Systems Instruments, Czech Republic) with blue or red excitation lights in 15 min intervals. The devices are further referred as BLE (blue light excitation) and RLE (red-light excitation) F-pens in the manuscript.

The rETR was calculated according to Juneau and Harrison (2005) as

$$rETR = \Phi_{PSII} \times PAR \qquad Eqn.\ 1,$$

where Φ_{PSII} is the effective quantum yield and PAR is the incident radiation.

Statistics

The tested null hypotheses were (a) there is no difference in T_{air} and PAR between the seasons, (b) there is no differences in the photosynthetic activity between the seasons, (c) there is no effect of T_{air} and PAR on *Vaucheria* sp. photosynthetic activity. The descriptive statistics, t-test and paired t-test were performed using the Statistica 13.0 software ([2] - Dell 2015). The multivariable analysis and generalized addition modules (GAM) creation were performed using CANOCO 5 software (Ter Braak and Šmilauer 2012). The results were considered statistically significant for $P<0.05$.

Results

Microclimate

The season 2016 was warmer than the season 2017 (paired t-test, n = 1032, t = 17.1, P<0.001; Fig. 1). In 2016, the maximum PAR was significantly higher in 2016 than in 2017, but the mean PAR was increased in 2017 (paired t-test, n = 1032, t = -3.49, P<0.001; Table 1, Fig. 1).

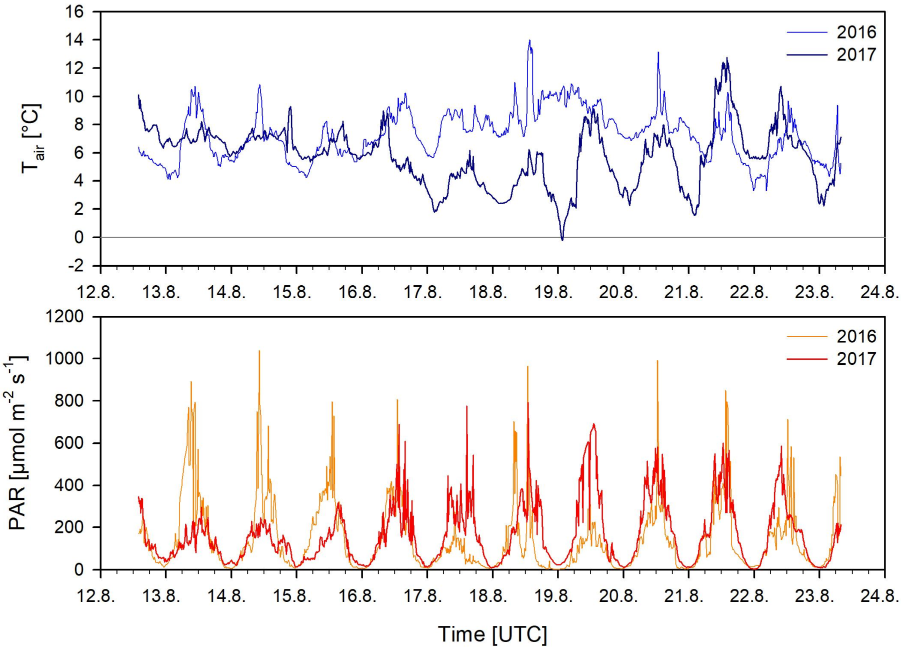

Fig. 1. The courses of air temperature (T_{air}) and photosynthetically active radiation (PAR) during the measurement periods in 2016 and 2017.

Photosynthetic activity

In 2016, the Φ_{PSII} values measured using the BLE F-pen were slightly lower than those measured by the RLE F-pen (paired t-test, n= 963, t = -9.77, P<0.001). Contrary, the Φ_{PSII} values measured using the BLE F-pen were slightly higher than those measured by the RLE F-pen (paired t-test, n= 776, t = 16.1, P<0.001). Similarly, the higher rETR values were measured by the RLE F-pen in 2016 (t-test, n= 963, t = -8.49, P<0.001) and by the BLE F-pen in 2017 (paired t-test, n= 776, t = 16.1, P<0.001) (Table 2).

The Φ_{PSII} and rETR values measured by the BLE F-pen were higher in 2017 (t-test, t = -9.95, P<0.001 for Φ_{PSII} and t = -23.7, P<0.001 for rETR). Contrary, the Φ_{PSII} values measured by the RLE F-pen were higher in 2016 (t-test, t = 3.63, P<0.001), but the rETR values were higher in 2017 (t-test, t= -18.2, P<0.001; Table 2). In both years, the photoinhibition was rare at high irradiances (Fig. 2). The lowest rETRs occurred in broad temperature ranges indicating thus the irradiance as main photosynthesis driver (Fig. 2).

	2016		2017	
T_{air} [°C] (mean ± s.d.)	7.3 ± 1.8		5.7 ± 2.1	
T_{min} [°C]	3.3	Aug 22, 04:30	-0.2	Aug 19 01:30
T_{max} [°C]	14.0	Aug 18, 13:30	12.8	Aug 21 14:00
PAR [µmol m^{-2} s^{-1}] (mean ± s.d.)	147 ± 166		165 ± 146	
PAR_{min} [µmol m^{-2} s^{-1}]	2	Aug 18, 22:30 Aug 18, 23:00 Aug 18, 23:15 Aug 18, 23:45	4	Aug 21, 23:45
PAR_{max} [µmol m^{-2} s^{-1}]	1037	Aug 14, 10:15	793	Aug 18 13:00

Table 1. The means, standard deviations, minima and maxima of air temperature (T_{air}, T_{min}, T_{max}) and photosynthetically active radiation (PAR, PAR_{min}, PAR_{max}) in summer seasons 2016 and 2017 (n = 1032 in each dataset) and dates nad times when the extremes were reached.

	2016		2017	
	BLE F-pen	RLE F-pen	BLE F-pen	RLE F-pen
Φ_{PSII} (mean ± s.d.)	0.488 ± 0.150	0.514 ± 0.134	0.550 ± 0.092	0.493 ± 0.101
$\Phi_{PSII\,min}$	0.000	0.000	0.201	0.000
$\Phi_{PSII\,max}$	0.662	0.701	0.711	0.746
rETR (mean±s.d.)	22.3 ± 18.4	26.1 ± 25.4	71.9 ± 61.5	61.9 ± 54.2
$rETR_{min}$	0.0	0.0	0.4	0.0
$rETR_{max}$	249	220.0	366.3	337.6

Table 2. The means, standard deviations, minima and maxima of Φ_{PSII} ($\Phi_{PSIImin}$, $\Phi_{PSIImax}$) and rETR ($rETR_{min}$, $rETR_{max}$) during summer seasons in 2016 and 2017 (n = 963 for 2016, n = 776 for 2017) measured using BLE and RLE" F-pens.

For the RDA analysis, only Φ_{PSII} was used, since the rETR values were derived from PAR as explanatory variable (*Eqn*. 1). The RDA analysis confirmed the PAR as the main driver of the photosynthetic activity, expressed as Φ_{PSII}, explaining 58.7% and 33.5% of total explained variability in 2016 and 2017, respectively (Fig. 3, Table 3). When both years were considered the explained variability was 25.2% (Fig. 3). The air temperature was as less important, since it explained 8.7% and 6.5% of total explained variation in 2016 and 2017, respectively, and 7.8% in both years (*see* Table 3).

The generalized addition modules (GAM) confirmed the negative correlation between the Φ_{PSII} and the PAR or T_{air} (Fig. 4). Slight differences were found between the BLE and RLE F-pens, but the trends were similar. However, when the rETR was considered, only a few cases of inhibition of photosynthetic activity were observed (*see* Fig. 2).

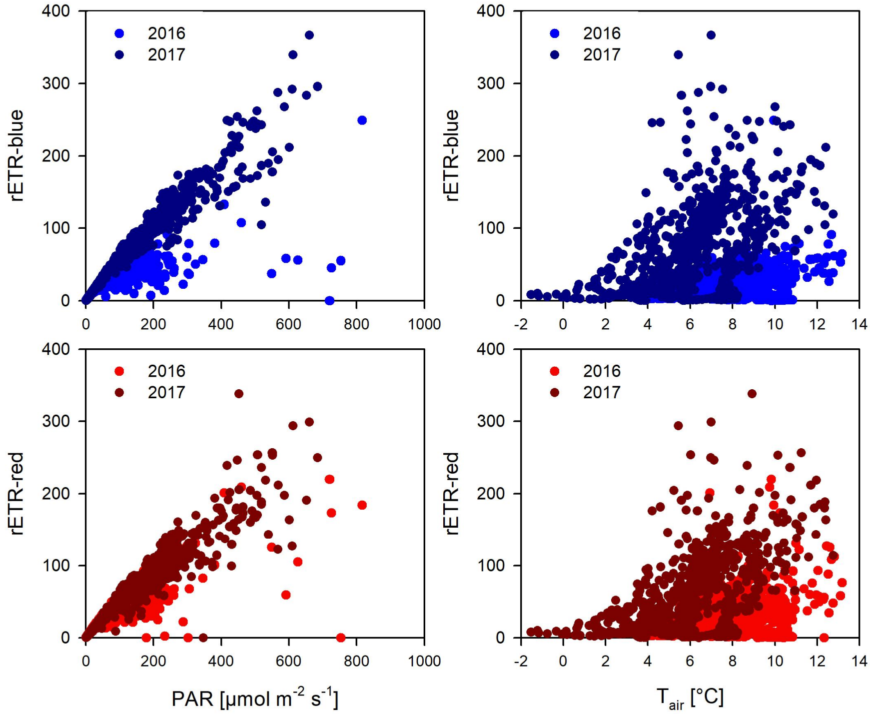

Fig. 2. The dependence relative electron transfer rate (rETR) on photosynthetically active radiation (PAR) or air temperature (T_{air}). -blue or -red colors refer to excitation light of given FluorPen.

Explanatory variables	2016	2017	2016 + 2017
Total variation	311.4	14.4	399.8
PAR +T_{air}			
Total explained variation	58.8%	35.4%	35.8%
Monte Carlo permutation test			
1^{st} axis	pseudo-F=1365, P=0.002	pseudo-F=404, P=0.002	pseudo-F=887, P=0.002
All axes	pseudo-F=684, P=0.002	pseudo-F=212, P=0.002	pseudo-F=322, P=0.002
PAR			
Total explained variation	58.7%	33.5%	25.2%
Monte Carlo permutation test			
All axes	pseudo-F=1366, P=0.002	pseudo-F=390, P=0.002	pseudo-F=584, P=0.002
T_{air}			
Total explained variation	8.7%	6.5%	7.8%
Monte Carlo permutation test			
All axes	pseudo-F=92.1, P=0.002	pseudo-F=54.1, P=0.002	pseudo-F=148, P=0.002

Table 3. The results of the RDA analysis for individual years (2016 and 2017) and both of them (2016 + 2018). The analysis for both years (2016 + 2017) was performed with year as a factor (n = 963 for 2016, n = 776 for 2017, n = 1739 for both years).

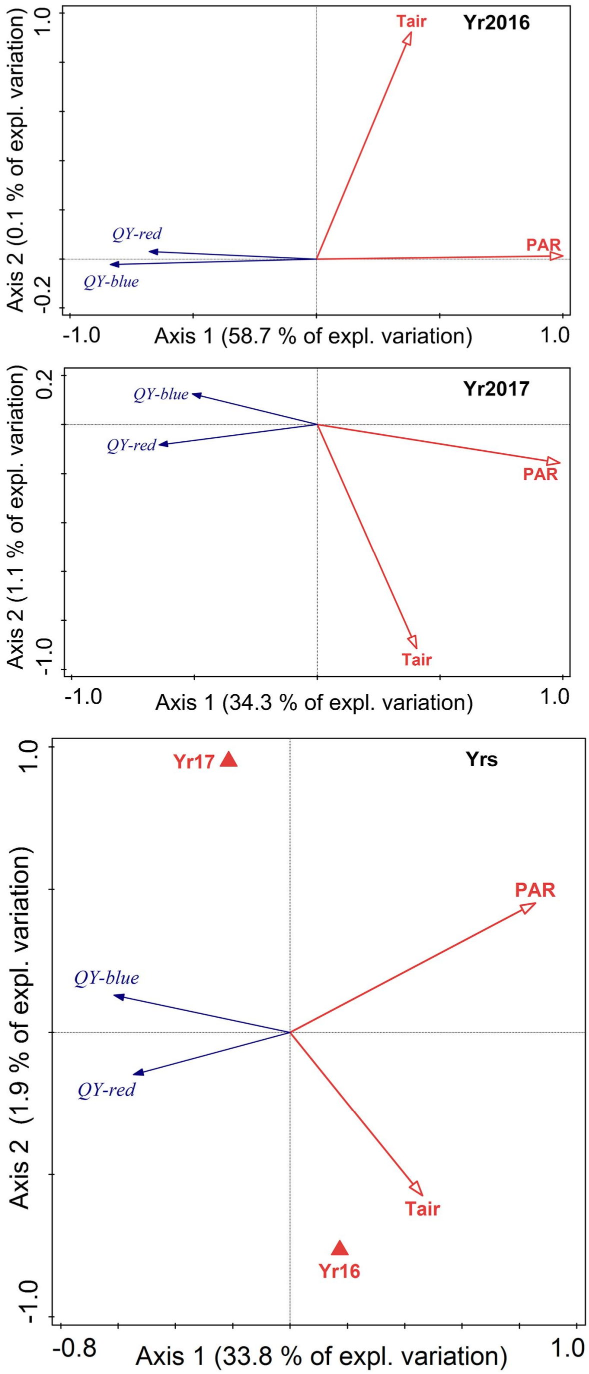

Fig. 3. The RDA analyses for summer season in 2016 (Yr2016), summer season in 2017 (Yr2017) and both seasons (Yrs). Abbreviations: PAR – photosynthetically active radiation; Tair – air temperature; QY – effective quatum yield; -blue or -red refers to excitation light in FluorPen used.

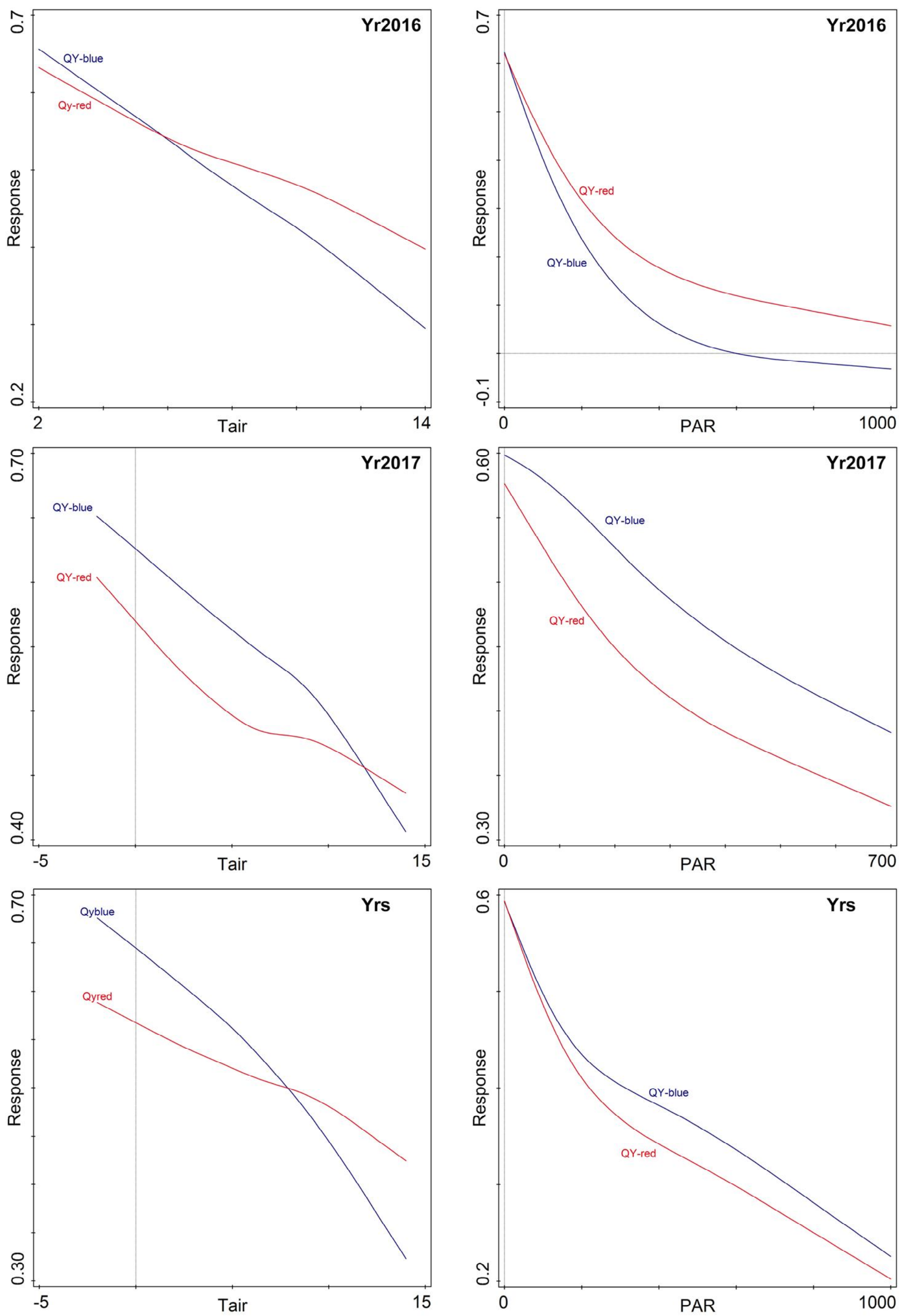

Fig. 4. The GAM for response of the effective quantum yield on (a) air temperature (T_{air}), and (b) photosynthetically active radiation (PAR) in summer season in 2016 (Yr2016), summer season in 2017 (Yr2017) and in both seasons (Yrs).

Discussion

The T_{air} and PAR values were typical for late Arctic summer in both years (Kvíderová and Elster 2017, Kvíderová et al. 2019, Láska et al. 2012). The comparison of the PAR and T_{air} proved inter-annual variation, however, these differences were only minor in general. The actual meteorological situation may play important role, since the course of the T_{air} were similar in periods between August 12 and August 17 and between August 21 and August 23, but they differed to a large extent between August 16 and 21. The lower mean T_{air} in 2017 was probably caused by cold period between the August 17 and 21, 2017, when the T_{air} had dropped even slightly below 0°C.

Since the minimal photosynthetic activity was observed in broad temperature ranges in both years (Fig. 2), the temperature does not seem to be the key factor in photosynthesis acclimation in *Vaucheria* sp. The low photosynthetic activity (Φ_{PSII},) was probably caused by very low PAR at local midnight or dense fog during the daytime.

The PAR was very variable in both years ranging from 0 to almost 1000 µmol m^{-2} s^{-1}, but the diel periodicity was apparent, as the polar day was near to the end. Although the PAR values exceeded 1000 µmol m^{-2} s^{-1} in 2016, the maximum PAR value was much lower in 2017. Despite the maximum PAR values in 2016, the mean PAR value in 2017 was higher, indicating thus mean lower total cloud cover and/or higher fraction of middle and high clouds in 2017, confirming thus the role of actual meteorological situation.

Despite of encountering relatively high PAR, the photoinhibition at high PAR (above 500 µmol m^{-2} s^{-1}) was found only occasionally in both years. No serious photoinhibition was found during at least 1 h lasting pre-acclimation of *Vaucheria* sp. thalli to 650 µmol m^{-2} s^{-1} in gasometric measurements in 2017 (Kvíderová et al. 2019). However, the rapidly changing light environment requires fast photoacclimation or tolerance to a broad range of PAR (Falkowski and LaRoche 1991, Falkowski and Raven 2007). Kvíderová et al. (2019) proved that *Vaucheria* sp. is pre-acclimated to prevailing low-light conditions typical for the polar regions (Clark et al. 2013).

The inter-annual comparisons showed increased photosynthetic activity in 2017 which could be caused either by higher PAR in 2017, or by the differences in microcosmos design, or even by combination of both factors. In 2016, complete benthic microbial community including sediment and sea water was enclosed in the microcosm (Kvíderová and Elster 2017), and the sediment particles deposited on *Vaucheria* sp. thali, reducing thus incoming PAR. Contrary in 2017, the thalli were washed before enclosure (Kvíderová et al. 2019), therefore the light attenuation by the sediment was eliminated. The fully submerged thalli could suffer from CO_2 limitation compared to air exposed one due to lack of seawater mixing and sediment deposition resulting thus in slower CO_2 diffusion. Slight reduction of photosynthetic activity was observed in fully-hydrated *Nostoc commune* s.l. colonies in comparison with partially desiccated ones (Kvíderová et al. 2011). Also, this difference may reflect spatial heterogeneity of the *Vaucheria* sp.-dominated microbial mat. The hypothesis of heterogeneity could be supported by the opposite response of the photosynthetic activity to blue and red fluorescence excitation light in both years.

The PAR was confirmed as the main driver of photosynthesis in late Artic summer, as already suggested by Kvíderová and Elster (2017) and Kvíderová et al. (2019). The light intensity indeed caused the shift of maximum photosynthesis of Antarctic marine phytoplankton from midday in spring to midnight in summer (Rivkin and Putt 1987), however the response may be species-specific (Rivkin and Putt 1988). Kvíderová et al. (2019) suggested that the main photosynthesis driver might change during the vegetation period: tidal cycles might be the main photosynthesis driver during polar day, but as the diel light cycles become more prominent near the polar day end and during the transition period from the polar day to polar day to polar night, PAR starts to be the main photosynthesis driver. This hypothesis on shifts of photosynthesis drivers reminds to be tested by direct *in situ* measurements in longer time period. The measurements should start when visible *Vaucheria* sp. mats develop on the surface in mid-July and they should last till beginning of polar night in late October. Dataloggers for recording temperature, PAR and presence of liquid water, and autonomous waterproof fluorometers for measurement of effective quantum yield should be used in proposed study.

In conclusion, the experiments in microcosm showed good tolerance of *Vaucheria* sp. to prevailing temperature and light conditions within the seasons. The data also showed rapid photoacclimation to PAR changes and indicated PAR to be the driving factor of *Vaucheria* sp. photosynthesis in late Arctic summer. These characteristics should be beneficial for survival in hypervariable environment of the tidal flat.

References

BELLINGER, B., UNDERWOOD, G., ZIEGLER, S. and GRETZ, M. (2009): Significance of diatom-derived polymers in carbon flow dynamics within estuarine biofilms determined through isotopic enrichment. *Aquatic Microbial Ecology,* 55: 169-187.

CLARK, G. F., STARK, J. S., JOHNSTON, E. L., RUNCIE, J. W., GOLDSWORTHY, P. M., RAYMOND, B. and RIDDLE, M. J. (2013): Light ‐ driven tipping points in polar ecosystems. *Global Change Biology,* 19: 3749-3761.

ELSTER, J. (1999): Algal versatility in various extreme environments. *In*: J. Seckbach (ed.): Enigmatic microorganisms and life in extreme environments. Kluwer Academic Publishers, pp. 215-227.

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 Princeton University Press, Princeton, 488 p.

GORBUSHINA, A. A., KRUMBEIN, W. E. (1999): The poikilotrophic micro-organism and its environment. *In*: J. Seckbach (ed.): Enigmatic microorganisms and life in extreme environments. Kluwer Academic Press, pp. 177-185.

JUNEAU, P., HARRISON, P. (2005): Comparison by PAM fluorometry of photosynthetic activity of nine marine phytoplankton grown under identical conditions. *Photochemistry and Photobiology,* 81: 649-653.

KVÍDEROVÁ, J., ELSTER, J. and ŠIMEK, M. (2011): *In situ* response of *Nostoc commune* s.l. colonies to desiccation in Central Svalbard, Norwegian High Arctic. *Fottea,* 11: 87-97.

KVÍDEROVÁ, J., ELSTER, J. (2017): Photosynthetic activity of Arctic *Vaucheria* (Xanthophyceae) measured in microcosmos. *Czech Polar Reports,* 7: 52-61.

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.

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: 297-318.

RIVKIN, R. B., PUTT, M. (1987): Diel periodicity of photosynthesis in polar phytoplankton: influence on primary production. *Science,* 238: 1285-1288.

RIVKIN, R. B., PUTT, M. (1988): Seasonal pattern of diel periodicity in photosynthesis by polar phytoplankton: species-specific response. *Journal of Phycology,* 24: 369-376.
SOUQUIERES, C.-E. (2018): Ecology and photosynthetic activity of a *Vaucheria* sp. dominated Arctic microphytobenthos, Svalbard. MSc. thesis. Universidade do Algarve, Algarve, 87 p.
SUNDBÄCK, K., MILES, A. and GÖRANSSON, E. (2000): Nitrogen fluxes, denitrification and the role of microphytobenthos in microtidal shallow-water sediments: an annual study. *Marine Ecology Progress Series,* 200: 59-76.
SZYMELFENIG, M., KWAŚNIEWSKI, S. and WĘSŁAWSKI, J. M. (1995): Intertidal zone of Svalbard. *Polar Biology,* 15: 137-141.
TER BRAAK, C. J. F., ŠMILAUER, P. (2012): Canoco reference manual and user's guide: software for ordination, version 5.0. v. Microcomputer Power, Ithaca, USA, 496 p.
WESLAWSKI, J., WIKTOR, J., ZAJACZKOWSKI, M. and SWERPEL, S. (1993): Intertidal zone of Svalbard. 1. Macroorganism distribution and biomass. *Polar Biology,* 13: 73-73.
WESLAWSKI, J., SZYMELFENIG, M. (1999): Community compositon of tidal flats on Spitsbergen: consequence of disturbance? *In*: J. S. Gray, W. Ambrose, A. Szaniawska (eds.): Biogeochemical cycling and sediment ecology. NATO ASI Series (Series E: Applied Sciences), vol 59. Springer, Dordrecht, pp. 185-193.
WIKTOR, J., TATAREK, A., WĘSŁAWSKI, J. M., KOTWICKI, L. and POULIN, M. (2016): Colonies of *Gyrosigma eximium*: a new phenomenon in Arctic tidal flats. *Oceanologia,* 58: 336-340.

Web sources / Other sources

[1] ACIA (2005): Impacts of warming climate: arctic climate impact assessment. Cambridge University Press, Cambridge, 1042 p.

[2] DELL, INC. (2015): Dell Statistica (data analysis software system), version 13. http://software.dell.com