

Low temperature inhibition of photosystems I, and II in Antarctic lichens of different morphotypes

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Abstract

Chlorophyll fluorescence techniques represent an effective tool for photosynthetic performance of extremophilic poikilohydric autotrophs from cold Earth regions. Many parameters of these techniques can detect the response of photosystem II (PS II) to a great variety of stressors. Chlorophyll fluorescence parameters related to PS II functioning are used quite often. For Antarctic lichens, that evolved several physiological mechanisms to cope with close to 0°C or even at sub-zero temperatures. The data gained from both field- and laboratory based studies helps predict ecophysiological consequences of episodic drops in *in situ* temperature as well as resistance of Antarctic terrestrial autotrophs to low temperature. However, the effect of low and sub-zero temperature on photosystem I (PS I) functioning is studied much less frequently than PS II. Therefore, the aim of our study was to evaluate PS II and PS I activities under low temperature and enlarge the knowledge on the low temperature effects on lichen photosynthesis. The focus of our laboratory experiments was to quantify the effect of a short-term treatment by 0°C on chlorophyll fluorescence parameters related to PS II and PS I functioning in two species of chlorolichens from Antarctica (*Usnea antarctica*, *Himantormia lugubris*). Our results suggest low temperature-induced decline in physiological processes in chloroplast (Performance index decrease) and activation of protective mechanisms (non-photochemical quenching increase).

Key words: *Himantormia*, *Usnea*, PS I, PS II, Nelson Island, chlorophyll fluorescence

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Introduction

Low temperature effect on primary photosynthetic processes associated with photosystem II (PS II) are well described for vascular plants as well as for poikilohydric mosses and lichens. In the latter ones, a decrease of thallus temperature below temperature optimum brings gradual inhibition of primary photosynthesis. Generally, lichens are resistant to low temperatures and present positive photosynthesis at temperatures close to 0°C (Schroeter and Scheidegger 1995). Some mosses and lichens, typically those from alpine and polar habitats are capable to maintain primary photosynthetic processes even at sub-zero temperature. In such Antarctic lichen species, the optimum temperature for net photosynthesis is between 5–15°C (Reiter *et al.* 2007). Within last decade, several studies have focused the response of PS II-related photosynthetic processes to low temperature in Antarctic lichens. They addressed a wide range of effects ranging from field ecophysiological studies (Cho *et al.* 2020) to cryoresistance studies focused on the evaluation of critical temperature of PS II-related processes, the chlorophyll fluorescence parameters F_v/F_m and Φ_{PSII} in particular (Andrzejowska *et al.* 2024). Antarctic lichens show critical temperature, *i.e.* the temperature at which PS II-related processes reach zero, far below 0°C as shown *e.g.* for effective quantum yield of photosynthetic processes in PS II (Φ_{PSII}): –10°C for *Usnea antarctica* (Hájek *et al.* 2022), and –26°C for *Placopsis contortuplicata* (Mishra *et al.* 2015).

In temperature close to 0°C, both primary photosynthetic (photochemical), and secondary photosynthetic processes are active since Antarctic lichens, thank to their adaptations and presence of antifreeze proteins and osmotically active biomolecules, are reported to perform photosynthesis at temperature far below 0°C (Kappen and Redon 1987). Underlying physiological

mechanisms are osmotically-controlled avoidance of cell and their organelles freezing, and keeping fluidity of thylakoid membrane of chloroplast including availability of liquid water in intrathalline space and photobiont cells (Haranczyk *et al.* 2021, Bacier *et al.* 2022).

It is well established that photoinhibition of photosystem I (PS I) might be triggered when plants are exposed to low temperature (Terashima *et al.* 1994). PS I activity under low temperature is studied mainly in chilling-sensitive plants, typically crops, and the effect of low temperature photoinhibition of PS I is evaluated by chlorophyll fluorescence techniques. Underlying physiological processes responsible for the low temperature PS I inhibition are reactive oxygen species ROS formation (Sejima *et al.* 2014) due to excess energy accumulation on the electron acceptor side of PS I. The formed ROS are highly reactive and inactivate PS I (Sonoi-ke 1996).

Recently, *MultispeQ* instrument has been used in ecophysiological studies, either alone or in combination with other instruments exploiting biophysical measurements (Ogbaga and Athar 2019). *MultispeQ* is designed for large-scale and widespread use in plant biology, especially because it measures non-photochemical quenching *sensu* Tietz (NPQ_t – Tietz *et al.* 2017), a parameter useful in the evaluation of early stages of stress in plant photosynthetic apparatus. Typical application of the *MultispeQ* approach is in phenotyping studies (*e.g.* Nepal *et al.* 2020, Fernández-Calleja *et al.* 2020) since the output parameters combine the following approaches: (1) chlorophyll fluorescence related to PS II functioning, (2) spectral reflectance, and also (3) evaluation of PS I activity. The approach of multiparametral analyses of the data gained by a *MultispeQ* instrument has been used to evaluation of the ef-

fect of environmental factors on plant physiological performance as reported for chilling temperature (Agarwal et al. 2023 – *Solanum lycopersicum*, Husain et al. 2023 – *Glycine max*), or reduced watering (Ben-Jabeur et al. 2021 – *Triticum aestivum*).

There are only limited number of studies focused on the effect of environmental factors on PS II functioning by exploiting a *MultispeQ* instrument and another fluorometer traditionally used in plant physiology and ecophysiology (Gudagno et al. 2021, Bharati et al. 2023). However, such studies address the relation between PS II and PS I functioning only scarcely (Woodford et al. 2024). Therefore, we hypothe-

sized PS II and PS I performance in chlorolichens should be similar to the response of isolated photobionts or model algal species (Caspary et al. 2021 for *Chlamydomonas reinhardtii*). To our best knowledge, the relation between PS II and PS I functioning has never been investigated in lichens, their respective algal/cyanobacterial intrathalline photobionts, exposed to low-temperature stress. Our study aims to investigate PS II- and PS I-related parameters in parallel during several temperature treatments to bring the some insight into PS II and PS I functioning at low temperature.

Material and Methods

Species collection and handling

Two species forming lichen cover in Antarctic vegetation oasis (Nelson Island, Antarctica) were selected for the experiments: *Himantormia lugubris*, and *Usnea antarctica*. They are quite abundant at the deglaciated northern part of the island (Rip Point, 62° 14' 15'' S, 58° 58' 45'' W) where they were collected in austral summer season 2022/2023. After collection, lichen thalli were dried out under natural conditions and transferred to the laboratories in the Czech Republic (Extreme Environments Laboratory, Masaryk university,

Brno, Czech Republic, CARP infrastructure). They were stored in dry state in a refrigerator at the temperature of 5°C. Before experiments, the thalli were re-wetted for 24 h under dim light and laboratory temperature (20°C). Five thalli per species were selected for the below-specified experiments according to the highest value of PS II capacity (F_v/F_m , measured by a FluorPen FP100, Photon systems Instruments, Drásov, Czech Republic) reached after re-wetting (data not shown).

Species specification

Himantormia lugubris is an antarctic endemic species with a complex thallus anatomy. It combines horizontal (young thallus, crustose part) and vertical thallus parts (old thallus) forming clusters (Sojo et al. 2003). Initial stages of thallus development (prothallus) is typically black. Older vertical strap-shaped thalli form a mass of chondroid mechanical tissue composed of conglutinated hyphae without symbiotic al-

gal photobionts. Vertically-arranged young thalli are regularly smooth and grey-cream coloured. In old thalli that have a complex 3-D structure showing a great variety of branching patterns the greyish surface is often disrupted and showing the black chondroid axis (Sancho et al. 2020). Some thalli have brown apothecia, sometimes very numerous in complex thalli, located on the top of the branches. Photo-

synthetic field studies are rather few addressing the species general photosynthetic performance (Sancho *et al.* 2020) response to manipulated warming of natural habitats (Marín *et al.* 2022).

Usnea antarctica is a species widely distributed in maritime Antarctica (Ott 2004). The species has a fruticose morphotype of thallus forming a complex branching structure up to 8 cm tall. Branches are sparingly to copiously divided. Surface of

thallus is typically yellow or brownish-yellow at base, variegated yellow with black at apices. The thallus surface is distinctly papillated or coarsely warted towards base. Photosynthetic studies carried out so far in the field addressed several aspects of the species response to environmental factors, such as temperature, light and water availability (Hovenden *et al.* 1994, Schroeter *et al.* 2021).

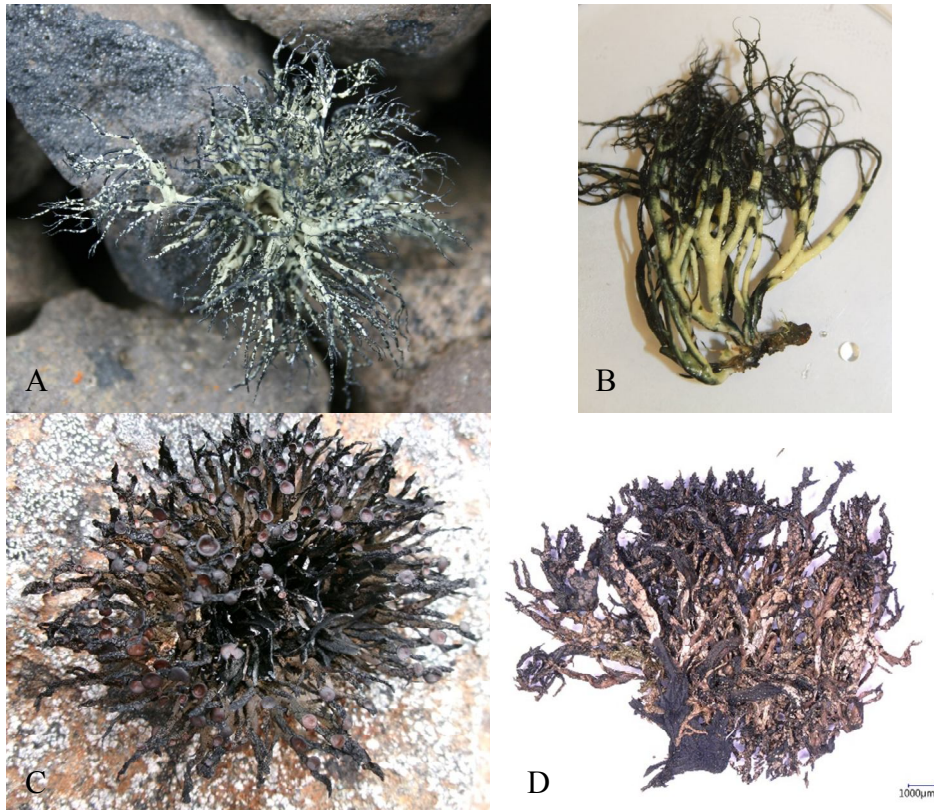


Fig. 1. Photographs of the experimental lichen species. Top view on a cluster of *Usnea antarctica* (A), and a detailed view on several individual branches - *U. antarctica*, side view (B). Top view on a cluster of *Himantormia lugubris* (C) showing numerous apothecia. Side view (D) of the same species shows a pattern of black (melanized) and brown thallus parts. Photos: CARP MUNI archive.

Exposition to low temperature

Before experiments, lichen thalli were placed into petri dishes rehydrated by demineralized water in between two sheets of paper for 48 h and the air temperature of 5°C. After the rewetting, physiological activity of individual thalli was checked by a FluorPen FP-100 fluorometer (Photon systems Instruments, Drásov, Czech Republic) and those thalli showing the highest F_v/F_m value were selected for experiments (5 thalli per species). Then, the samples (individual thalli) of the ex-

perimental lichen species were placed into a small-volume temperature controlled chamber (type URAS 4, Hartmann & Braun Germany) and exposed to a temperature treatment in the following sequence: (1) exposition to 20°C for 1 h, followed by (2) 10°C for 1 h, (3) 0°C for 1 h, and recovery at (4) 20°C for 1 h. At the end each above-specified exposition time, chlorophyll fluorescence parameters related to PS I and PS II activity (*see below*) were measured.

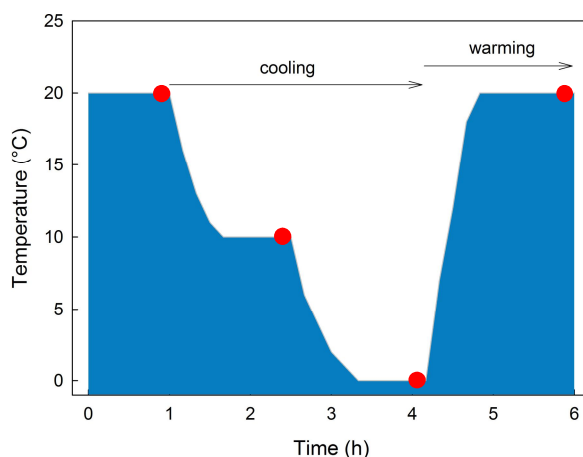


Fig. 2. Schematic chart of the temperature treatments used during experiment. The red dots indicate the time of the chlorophyll fluorescence measurements.

Chlorophyll fluorescence parameters in response to temperature

To evaluate low temperature effects on photosynthetic performance of PS II, fast chlorophyll fluorescence transients (OJIPs) were measured by a *FluorPen FP100* and the two following chlorophyll fluorescence parameters evaluated:

PI_{ABS}	Performance index
ET_0/RC	Electron transport rate per PS II reaction centre

The two parameters have the following meanings: (1) PI_{ABS} is a potential for energy conservation from exciton to reduction of intersystem electron acceptors, and (2) ET_0/RC is electron transport flux per PS II reaction centre. The equations of Strasser et al. (2000) were used for calculation of PI_{ABS} and ET_0/RC (Table 1).

We used a *MultispeQ* spectrophotometer (PhotosynQ LLC, East Lansing, Michigan, USA) for the measurements of other two selected parameters. One parameter relates to PS I (PS I overreduced centres), the other one to activation of PS II protective mechanisms (non-photochemical quenching, NPQ_t). Among measured and calculated parameters we selected the following two in order to evaluate the effect of particular experimental temperature on PS I and PS II functioning.

Parameter	Equation	Source
PI _{ABS}	$PI_{ABS} = (RC/ABS)[\phi Po / (1 - \phi Po)][\Psi o / (1 - \Psi o)]$	Strasser et al. (2000)
ET ₀ /RC	$ET_0/RC = MO (1/VJ) \psi Eo$	Strasser et al. (2000)
PS I overreduced centres		<i>MultispeQ</i>
NPQ _t	$NPQ_{(T)} = \frac{4.88}{\left(\frac{F'_m}{F_0}\right) - 1} - 1$	Tietz et al. (2017)

Table 1. Characterization of the parameters used in this study including the equations used in the calculations of their numeric values.

Results

Performance index (PI_{ABS}) decreased with the decrease of experimental temperature in both species. The low temperature-induced decline in PI_{ABS} was, however, more pronounced at *Usnea* sp. than *Himantormia lugubris*. At 0°C, PI_{ABS} value was lowest in *U. antarctica* showing the value of 0.016, contrastingly to *H. lugubris* which showed no change in PI_{ABS} if the values recorded at 20 and 0°C are compared.

Photosynthetic electron transport rate per reaction centre (ET₀/RC) decreased with the thallus temperature decline from 20 to 0°C, more apparently in *U. antarctica* where ET₀/RC dropped to 36.7% of maximum found at 20°C. In *H. lugubris* measured at 0°C, the ET₀/RC value reached 57.1% of maximum recorded at 20°C. Partial recovery of ET₀/RC was found for *U. antarctica* when exposed to 20°C after 1 h at 0°C. The recovery reached 59.6% of maximum ET₀/RC recorded at the very beginning of the experiment at 20°C. Contrastingly, *H. lugubris* showed no recovery of ET₀/RC, when exposed to 20°C again.

Both in *Usnea* sp. and *Himantormia lugubris*, the parameter PS I overreduced centres showed an increase with the thallus temperature drop from 20 to 10°C, followed by a remarkable decrease found for 0°C. Recovery of the thalli at 20°C led to an increase of the parameter. At the end of the exposition to 20°C, the increase PS I overreduced centres reach initial values. Therefore, recovery of PS I overreduced centres was completed in both experimental species.

Involvement of protective mechanisms (non-photochemical quenching, NPQ_t) during the low temperature treatment, however, differed between the two species. While it showed an increase of about 12% when measured at 0°C (compared to initial 20°C) in *U. antarctica*, there was almost no change in NPQ_t in *H. lugubris* when measured at 0°C (compared to initial 20°C). Effective involvement of protective NPQ in *U. antarctica* was documented by full relaxation of NPQ_t values, when the species was transferred to 20°C again. NPQ_t dropped to initial values in *U. antarctica*

at the end of measurements at 20°C. *H. lugubris*, contrastingly to *U. antarctica*, exhibited more or less constant NPQ_t values throughout all experimental tempera-

tures. Therefore, no change in NPQ_t values was apparent when the species was measured again at 20°C.

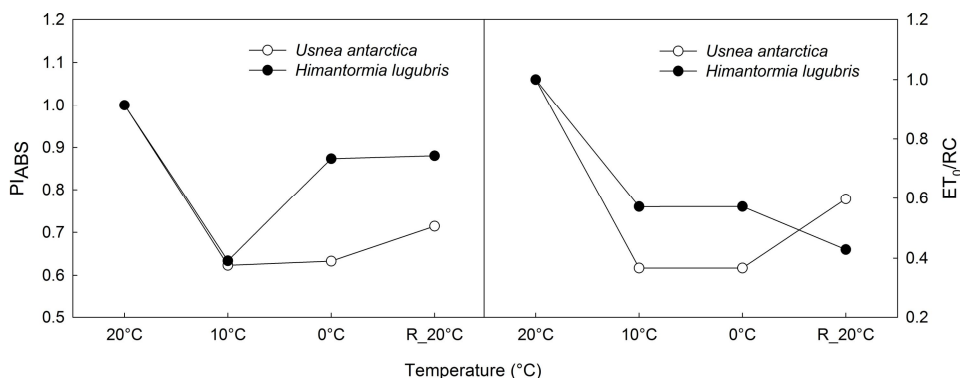


Fig. 3. Chlorophyll fluorescence parameters (normalized to initial value recorded at the beginning of experiment) derived from fast chlorophyll fluorescence transient (OJIP) as dependent on thallus temperature. The data points represent means of 5 replicates. *Left*: Performance index (PI_{ABS}), *right*: Electron transport rate per reaction centre (ET₀/RC).

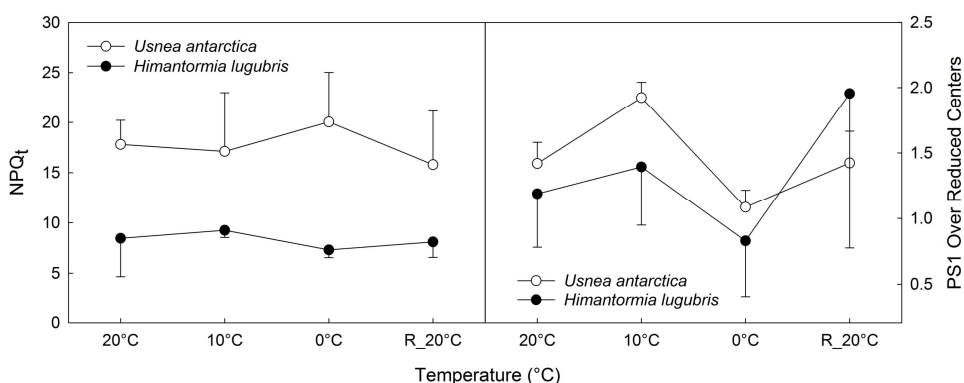


Fig. 4. The parameters (absolute values) measured by a *MiltispeQ* instrument as dependent on thallus temperature. The data points represent means of 3 replicates and standard deviations are indicated by error bars. *Left*: non-photochemical quenching (NPQ_t), *right*: PS I overreduced centers.

Discussion

PI_{ABS} responded to sequential decrease of thallus temperature (20, 10, 0°C) by a decrease found in both lichen species. The response is in agreement with previous

study of Bednaříková et al. (2020) that reported a decrease of 21% (*Xanthoria elegans*) and 35% (*Usnea antarctica*) in PI_{ABS} when data taken in 20°C and 0°C are

compared. Similar results are reported in earlier study (Marečková *et al.* 2019) for low temperature treated *Dermatocarpon polyphyllizum* in dark (exclusive low temperature effect, -5°C) and light-adapted lichen (low temperature plus light). In the study, PI_{ABS} decreased to 90% in the lichen thallus treated in dark, while more apparent decrease (to 75%) was found for the thallus treated in light (the decrease is related to the reference taken at 18°C). In general, PI_{ABS} is a sensitive indicator of overall physiological status of poikilohydric autotrophs from polar and alpine regions since it responds sensitively to thallus rehydration during drought stress. The PI_{ABS} is reported to decline in desiccating mosses (Giudici 2021). Moreover, PI_{ABS} decline with the strength and duration of high light-induced photoinhibition of photosynthetic processes as reported for Antarctic moss *Sanionia uncinata* (Orekhova *et al.* 2021).

The OJIP-derived parameter ET_0/RC is considered reliable for exploring the effect of changes in PS II activity under low temperature (Marečková *et al.* 2019) and light (Janeeshma *et al.* 2022). In general, a decrease in ET_0/RC is accompanied by a decrease in effectiveness of energy flow through PS II, and is reflected in a decrease of the parameters associated with PS II functioning, such as *e.g.* effective quantum yield of PS II. Temperature decrease-induced decline in effective quantum yield of PS II (Φ_{PSII}) was reported by Barták *et al.* (2007) in two Antarctic chlorolichens, and also by Hájek *et al.* (2021) for two Antarctic representatives of Usneaceae family. In the studies devoted to photosynthetic processes in lichens, Φ_{PSII} is considered a general indicator of primary photosynthesis. It is affected by a wide variety of environmental factors, since it reflects the (photosynthetic) electron transport rate between PS II and PS I, as well as the rate of utilization of NADPH and ATP in biochemical photosynthetic processes (Calvin-Benson cycle). During a

light period of a day, low temperature reduces the rate of CO_2 fixation. The reduction leads to substantial decrease of NADPH^+ in chloroplasts. Since NADPH^+ is a major acceptor of electrons in PS I, the decrease leads to overreduction on PS I acceptor side as well as hydroxyl radicals formation (Mi *et al.* 2000).

Non-photochemical quenching increased at 0°C in *Usnea antarctica* similarly as found in earlier studies (Hájek *et al.* 2022, Barták *et al.* 2007). Such increase in NPQ_t indicates low temperature-induced involvement of quenching mechanisms. In *U. antarctica*, the NPQ_t increase might be attributed to low temperature effect *per se* (Marečková *et al.* 2019) since the lichen thalli were exposed to low temperature in dark. Therefore, involvement of light-driven component of NPQ, *i.e.* photoinhibitory quenching (qI) might be omitted. The NPQ increase found in 0°C -treated *U. antarctica* might rather be attributed to low temperature-induced changes in structure of pigment-protein complexes forming PS II as well as changes in thylakoid membrane structure. The latter changes might be associated with direct temperature effects on lipids, and the change in unsaturated/saturated fatty acids. Antarctic lichens, their photobionts respectively, however, have developed several mechanisms to adjust membrane lipid and fatty acid composition to maintain membrane fluidity in the cold. Unsaturation of lipids in chloroplast is a general mechanism stabilizing membrane in chloroplast at low temperature (Moon *et al.* 1995). Importance of NPQ in Antarctic autotrophs adapted to low temperature has been emphasised just recently for photostasis in chloroplast (Hüner *et al.* 2024). NPQ increase is considered a general plant response during acclimation to low temperature. In Antarctic terrestrial autotrophs, however, both increase (Marečková *et al.* 2019) and decrease (Perera-Castro *et al.* 2020 – for mosses) in NPQ at the temperature close to 0°C are reported. Laboratory-based ex-

periments under fully-controlled conditions can be recommended for future research. They should involve NPQ response in Antarctic terrestrial autotrophs to low temperature photoinhibition. Moreover, a detailed analysis of the components forming NPQ, *i.e.* energy-dependent quenching (qE), photoinhibitory quenching (qI), and state-transition quenching (qT) should be done as well.

PS I overreduction decreased at 0°C (compared to a 20°C reference) in both experimental species which might be associated with low temperature-induced oxidation of PS I (*see* the below paragraph). Generally, the electron acceptor side of PS I is overreduced when the Calvin-Benson cycle cannot follow the production of NADPH which is dependent on the photosynthetic electron transport from PS II to PS I (Shimakawa and Miyake 2018). The over reduction of PS I may be partly alleviated by the activation of ferredoxin-NADP(+)-oxidoreductase or Mehler-peroxidase reaction leading to the fast reoxidation of electron carriers in thylakoid membranes (Ilik et al. 2006). Similarly, flavodiiron proteins have an important role in preventing PS I overreduction when plants are exposed to light. Flavodiiron proteins are reported for algae, cyanobacteria, but not angiosperm plants. They sustain an alternative pathway transferring electrons downstream PS I to O₂ as a final acceptor with the formation of H₂O (Gerotto et al. 2016, Storti et al. 2020).

It is well established that oxidation of PS I leading to its oxidized state (P700⁺) represents one of the strategies of keeping photosynthetic apparatus in chloroplast functioning at low and chilling temperature throughout plant kingdom (Sunoj et al. 2023). Such low temperature-induced

protection of PS I from oxidative damage by keeping PS I in an oxidized state (P700⁺) is crucial to the survival of plants exposed to light at low or close-to-zero temperature (Miyake 2020) including low temperature photoinhibition of PS I (Virtanen et al. 2020). Underlying physiological mechanism activated in such situation is cyclic electron transport (Kubo et al. 2011). Our data, however, does not support the idea of PS I oxidation at 0°C (compared to 20°C) since the parameter P700⁺ showed scattered values with no clear trend (data not shown). This might be caused by the experimental design, which focused on PS I response to low temperature *per se*, *i.e.* with exclusion of interacting light. Therefore, the changes in PS I overreduced centres (Fig. 4) were related exclusively to temperature drop but not to the phenomenon of low temperature photoinhibition in the two studied lichen species. However, PS I changes have been studied in response to desiccation stress in lichens by (Bukhov et al. 2004) who reported two components of dark re-reduction of oxidized PS I (P700⁺ caused by desiccation stress). On the other hand, an increase PS I overreduced centres (measured by a *MultispeQ*) might be associated with some positive effects on photosynthesis since Li et al. (2023) report stimulating effect of blue light on both PS II effectivity indicators (F_V/F_M, Φ_{PSII}, qL) and PS I overreduced centres. On the other hand, Gupta et al. (2024) reported that parameter PS I overreduced centers was negatively correlated to both PC 1 and PC 2 (principal component analysis). Our data obtained for *U. antarctica* and *H. lugubris* at 0°C indicate low temperature-induced PS I inactivation.

Concluding remarks

Low temperature PS I photoinhibition is mainly avoided by activation of several

protective mechanisms. Therefore, the phenomenon should be studied by biophysi-

cal methods exploiting chlorophyll fluorescence in combination with biochemical methods evaluating capacity of anti-oxidants in response to controlled low-temperature photoinhibition.

References

- AGARWAL, T., WANG, X., MILDENHALL, F., IBRAHIM, I. M., PUTHIYAVEETIL, S. and VARALA, K. (2023): Chilling stress drives organ-specific transcriptional cascades and dampens diurnal oscillation in tomato. *Horticulture Research*, 10(8): uhad137. doi: 10.1093/hr/uhad137
- ANDRZEJOWSKA, A., HÁJEK, J., PUHOVKIN, A., HARAŇCZYK, H. and BARTÁK, M. (2024): Freezing temperature effects on photosystem II in Antarctic lichens evaluated by chlorophyll fluorescence. *Journal of Plant Physiology*, 294: 154192. doi: 10.1016/j.jplph.2024.154192
- BACIOR, M., HARAŇCZYK, H., NOWAK, P., KIJAK, P., MARZEC, M., FITAS, J. and OLECH, M. (2022): Low-temperature investigation of residual water bound in free-living Antarctic *Prasiola crispa*. *Antarctic Science*, 34(5): 389-400. doi:10.1017/S0954102022000335
- BARTÁK, M., VÁCZI, P., HÁJEK, J. and SMYKLA, J. (2007): Low-temperature limitation of primary photosynthetic processes in Antarctic lichens *Umbilicaria antarctica* and *Xanthoria elegans*. *Polar Biology*, 31(1): 47-51. doi: 10.1007/s00300-007-0331-x
- BEDNAŘÍKOVÁ, M., FOLGAR-CAMEÁN, Y., KUČEROVÁ, Z., LAZÁR, D., ŠPUNDOVÁ, M., HÁJEK, J. and BARTÁK, M. (2020): Special issue in honour of Prof. Reto J. Strasser – Analysis of K- and L-band appearance in OJIPs in Antarctic lichens in low and high temperature. *Photosynthetica*, 58(SI): 646-656. doi: 10.32615/ps.2019.180
- BEN-JABEUR, M., ROMERO, A. G., VICENTE, R., KTHIRI, Z., KEFAUVER, S. C., SERRET, M. D., ARAUS, J. and HAMADA, W. (2021): MultispeQ for tracing biostimulants effect on growth promoting and water stress tolerance in wheat. Cham: Springer International Publishing. In: Recent Advances in Environmental Science from the Euro-Mediterranean and Surrounding Regions (2nd Edition) Proceedings of 2nd Euro-Mediterranean Conference for Environmental Integration (EMCEI-2), Tunisia 2019.
- BHARATI, R., GUPTA, A., NOVY, P., SEVEROVÁ, L., ŠRÉDL, K., ŽIAROVSKÁ, J. and FERNÁNDEZ-CUSIMAMANI, E. (2023): Synthetic polyploid induction influences morphological, physiological, and photosynthetic characteristics in *Melissa officinalis* L. *Frontiers in Plant Science*, 14: 1332428. doi: 10.3389/fpls.2023.1332428
- BUKHOV, N. G., GOVINDACHARY, S., EGOROVA, E. A. and CARPENTIER, R. (2004): Recovery of photosystem I and II activities during re-hydration of lichen *Hypogymnia physodes* thalli. *Planta*, 219(1): 110-120. doi: 10.1007/s00425-003-1195-0
- CASPY, I., SCHWARTZ, T., BAYRO-KAISER, V., FADEEVA, M., KESSEL, A., BEN-TAL, N. and NELSON, N. (2021). Dimeric and high-resolution structures of Chlamydomonas Photosystem I from a temperature-sensitive Photosystem II mutant. *Communications Biology*, 4(1): 1380. doi: 10.1038/s42003-021-02911-7
- CHO, S. M., LEE, H., HONG, S. G. and LEE, J. (2020): Study of ecophysiological responses of the antarctic fruticose lichen *Cladonia borealis* using the PAM fluorescence system under natural and laboratory conditions. *Plants* (Basel, Switzerland), 9(1): 85. doi: 10.3390/plants9010085
- FERNÁNDEZ-CALLEJA, M., MONTEAGUDO, A., CASAS, A. M., BOUTIN, C., PIN, P. A., MORALES, F. and IGARTUA, E. (2020): Rapid On-site phenotyping via field fluorimeter detects differences in photosynthetic performance in a hybrid-parent barley germplasm set. *Sensors* (Basel, Switzerland), 20(5): 1486. doi: 10.3390/s20051486
- GEROTTO, C., ALBORESI, A., MENEGHESSO, A., JOKEL, M., SUORSA, M., ARO, E. M. and MOROSINOTTO, T. (2016): Flavodiiron proteins act as safety valve for electrons in *Physcomitrella patens*. *Proceedings of the National Academy of Sciences of the United States of America*, 113(43): 12322-12327. doi: 10.1073/pnas.1606685113

- GUADAGNO, C. R., BEVERLY, D. P. and EWERS, B. E. (2021): The love-hate relationship between chlorophyll a and water in PSII affects fluorescence products. *Photosynthetica*, 59(SI): 409-421. doi: 10.32615/ps.2021.023
- GUIDICI, G. N. M. (2021): Combined chlorophyll fluorescence techniques to study environmental impact on the mountain moss *Polytrichum commune*. *Czech Polar Reports*, 11(1): 161-173.
- GUPTA, A., BHARATI, R., KUBES, J., POPELKOVÁ, D., PRAUS, L., YANG, X., SEVEROVA, L., SKALICKY, M. and BRESTIC, M. (2024): Zinc oxide nanoparticles application alleviates salinity stress by modulating plant growth, biochemical attributes and nutrient homeostasis in *Phaseolus vulgaris* L. *Frontiers in Plant Science*, 15: 1432258. doi: 10.3389/fpls.2024.1432258
- HÁJEK, J., HOJDOVÁ, A., TRNKOVÁ, K., VÁCZI, P., BEDNÁŘIKOVÁ, M. and BARTÁK, M. (2021): Responses of thallus anatomy and chlorophyll fluorescence-based photosynthetic characteristics of two Antarctic species of genus *Usnea* to low temperature. *Photosynthetica*, 59(1): 95-105.
- HÁJEK, J., PUHOVKIN, A., GIORDANO, D. and SEKERÁK, J. (2022): What does critical temperature tell us about the resistance of polar lichens to freezing stress? Applicability of linear cooling method to ecophysiological studies. *Czech Polar Reports*, 12(2): 246-255. doi: 10.5817/CPR2022-2-18
- HARAŇCZYK, H., STRZÁŁKA, K., KUBAT, K., ANDRZEJOWSKA, A., OLECH, M., JAKUBIEC, D., KIJAK, P., PALFNER, G. and CASANOVA-KATNY, A. (2021): A comparative analysis of gaseous phase hydration properties of two lichenized fungi: *Niebla tigrina* (Follman) Rundel & Bowler from Atacama Desert and *Umbilicaria antarctica* Frey & I. M. Lamb from Robert Island, Southern Shetlands Archipelago, maritime Antarctica. *Extremophiles: life under extreme conditions*, 25(3): 267-283. doi: 10.1007/s00792-021-01227-y
- HOVENDEN, M., JACKSON, A. E. and SEPPELT, R.D. (1994): Field photosynthetic activity of lichens from the Windmill Island oasis, Wilkies land, Continental Antarctica. *Physiologia Plantarum*, 90: 567-576.
- HÜNER, N. P. A., IVANOV, A. G., SZYSZKA-MROZ, B., SAVITCH, L. V., SMITH, D. R. and KATA, V. (2024): Photostasis and photosynthetic adaptation to polar life. *Photosynthesis Research*, 161(1-2): 51-64. doi: 10.1007/s11120-024-01104-7
- HUSSAIN, M. A., LI, S., GAO, H., FENG, C., SUN, P., SUI, X., JING, Y., XU, K., ZHOU, Y., ZHANG, W., and LI, H. (2023): Comparative analysis of physiological variations and genetic architecture for cold stress response in soybean germplasm. *Frontiers in Plant Science*, 13: 1095335. doi: 10.3389/fpls.2022.1095335
- ILÍK, P., SCHANSKER, G., KOTABOVÁ, E., VÁCZI, P., STRASSER, R. J. and BARTÁK, M. (2006): A dip in the chlorophyll fluorescence induction at 0.2-2 s in *Trebouxia*-possessing lichens reflects a fast reoxidation of photosystem I. A comparison with higher plants. *Biochimica et Biophysica Acta*, 1757(1): 12-20. doi: 10.1016/j.bbabi.2005.11.008
- JANEESHMA, E., JOHNSON, R., AMRITHA, M. S., NOBLE, L., ASWATHI, K. P. R., TELESÍŃSKI, A., KALAJI, H. M., AURIGA, A. and PUTHUR, J. T. (2022): Modulations in chlorophyll a fluorescence based on intensity and spectral variations of light. *International Journal of Molecular Sciences*, 23(10): 5599. doi: 10.3390/ijms23105599
- KAPPEN, L., REDON, J. (1987): Photosynthesis and water relations of three maritime antarctic lichen species. *Flora*, 179(3): 215-229. doi: 10.1016/S0367-2530(17)30240-2
- KUBO, S., MASUMURA, T., SAITO, Y., FUKAYAMA, H., SUZUKI, Y., SUGIMOTO, T., MAKINO, A., AMAKO, K. and MIYAKE, C. (2011): Cyclic electron flow around PSI functions in the photoinhibited rice leaves. *Soil Science and Plant Nutrition*, 57(1): 105-113. doi: 10.1080/00380768.2011.553803
- LI, K., JI, L., XING, Y., ZUO, Z. and ZHANG, L. (2023): Data-independent acquisition proteomics reveals the effects of red and blue light on the growth and development of moso bamboo (*Phyllostachys edulis*) seedlings. *International Journal of Molecular Sciences*, 24(6): 5103. doi: 10.3390/ijms24065103
- MAREČKOVÁ, M., BARTÁK, M. and HÁJEK, J. (2019): Temperature effects on photosynthetic performance of Antarctic lichen *Dermatocarpon polyphyllizum*: A chlorophyll fluorescence study. *Polar Biology*, 42: 685-701. doi: 10.1007/s00300-019-02464-w

- MARÍN, C., BARTÁK, M., PALFNER, G., VERGARA-BARROS, P., FERNANDOY, F., HÁJEK, J. and CASANOVA-KATNY, A. (2022): Antarctic lichens under long-term passive warming: Species-specific photochemical responses to desiccation and heat shock treatments. *Plants* (Basel, Switzerland), 11(19): 2463.
- MI, H., KLUGHAMMER, C. and SCHREIBER, U. (2000): Light-induced dynamic changes of NADPH fluorescence in *Synechocystis* PCC 6803 and its *ndhB*-defective mutant M55. *Plant & Cell Physiology*, 41(10): 1129-1135. doi: 10.1093/pcp/pcd038
- MISHRA, A., HÁJEK, J., TUHÁČKOVÁ, T., BARTÁK, M. and MISHRA K. B. (2015): Features of chlorophyll fluorescence transients can be used to investigate low temperature-induced effects on photosystem II of algal lichens from polar regions. *Czech Polar Reports*, 5(1): 99-111. 10.5817/CPR2015-1-10
- MIYAKE C. (2020): Molecular mechanism of oxidation of P700 and suppression of ROS production in photosystem I in response to electron-sink limitations in C3 plants. *Antioxidants* (Basel, Switzerland), 9(3): 230. doi: 10.3390/antiox9030230
- MOON, B. Y., HIGASHI, S., GOMBOS, Z. and MURATA, N. (1995): Unsaturation of the membrane lipids of chloroplasts stabilizes the photosynthetic machinery against low-temperature photoinhibition in transgenic tobacco plants. *Proceedings of the National Academy of Sciences of the United States of America*, 92(14): 6219-6223. doi: 10.1073/pnas.92.14.6219
- NÉPAL, N., YACTAYO-CHANG, J. P., GABLE, R., WILKIE, A., MARTIN, J., ANIEMENA, C. L., GAXIOLA, R. and LORENCE, A. (2020): Phenotypic characterization of *Arabidopsis thaliana* lines overexpressing *AVP1* and *MIOX4* in response to abiotic stresses. *Applications in Plant Sciences*, 8(8): e11384. doi: 10.1002/aps3.11384
- OGBAGA, C. C., ATHAR, H. U. R. (2019): Inclusion of photoprotective parameters in photosynthesis-measuring systems to improve the interpretation of photosynthesis and productivity. *Photosynthetica*, 57(2): 712-713. doi: 10.32615/ps.2019.041
- OREKHOVA, A., BARTÁK, M., CASANOVA-KATNY, A. and HÁJEK, J. (2021): Resistance of Antarctic moss *Sanionia uncinata* to photoinhibition: Chlorophyll fluorescence analysis of samples from the western and eastern coasts of the Antarctic Peninsula. *Plant Biology* (Stuttgart, Germany), 23(4): 653-663. doi: 10.1111/plb.13270
- OTT, S. (2004): Early stages of development in *Usnea antarctica* Du Rietz in the South Shetland Islands, northern maritime Antarctica. *The Lichenologist*, 36(6): 413-423. doi: 10.1017/S0024282904014380
- PERERA-CASTRO, A. V., WATERMAN, M. J., TURNBULL, J. D., ASHCROFT, M. B., MCKINLEY, E., WATLING, J. R., BRAMLEY-ALVES, J., CASANOVA-KATNY, A., ZUNIGA, G., FLEXAS, J. and ROBINSON, S. A. (2020): It is hot in the sun: Antarctic mosses have high temperature optima for photosynthesis despite cold climate. *Frontiers in Plant Science*, 11: 1178. doi: 10.3389/fpls.2020.01178
- REITER, R., GREEN, A. T. G., SCHROETER, B. and TÜRK, R. (2007): Photosynthesis of three *Umbilicaria* species from lichen dominated communities of the alpine/nival belt of the Alps measured under controlled conditions. *Phyton*, 46(2): 247-258.
- SANCHO, L., DE LOS RÍOS, A., PINTADO, A., COLESIE, C., RAGGIO, J., ASCASO, C. and GREEN, A. (2020): *Himantormia lugubris*, an Antarctic endemic on the edge of the lichen symbiosis. *Symbiosis*, 82(1, SI): 49-58. doi: 10.1007/s13199-020-00723-7
- SEJIMA, T., TAKAGI, D., FUKAYAMA, H., MAKINO, A. and MIYAKE, C. (2014): Repetitive short-pulse light mainly inactivates photosystem I in sunflower leaves. *Plant & Cell Physiology*, 55(6): 1184-1193. doi: 10.1093/pcp/pcu061
- SHIMAKAWA, G., MIYAKE, C. (2018): Oxidation of P700 ensures robust photosynthesis. *Frontiers in Plant Science*, 9: 1617. doi: 10.3389/fpls.2018.01617
- SCHROETER B., SCHEIDEGGER C. (1995): Water relations in lichens at subzero temperatures: Structural changes and carbon dioxide exchange in the lichen *Umbilicaria aprina* from continental Antarctica. *New Phytologist*, 131: 275-285. doi: 10.1111/j.1469-8137.1995.tb05729.x
- SCHROETER, B., GREEN, T. G., PINTADO, A., TÜRK, R. and SANCHO, L. G. (2021): Summer activity patterns for a moss and lichen in the maritime Antarctic with respect to altitude. *Polar Biology*, 44(11): 2117-2137. doi: 10.1007/s00300-021-02939-9

- SOJO, F., ROMEIKE, J. and OTT, S. (2003): *Himantormia lugubris* (Hue) M. Lamb – vegetative and reproductive habit: Adaptations of an Antarctic endemic. *Flora*, 198: 118-126.
- SONOIKE, K. (1996): Photoinhibition of Photosystem I: Its physiological significance in the chilling sensitivity of plants. *Plant and Cell Physiology*, 37(3): 239-247.
- STORTI, M., PUGGIONI, M. P., SEGALLA, A., MOROSINOTTO, T. and ALBORESI, A. (2020): The chloroplast NADH dehydrogenase-like complex influences the photosynthetic activity of the moss *Physcomitrella patens*. *Journal of Experimental Botany*, 71(18): 5538-5548. doi: 10.1093/jxb/eraa274
- STRASSER, R. J., SRIVASTAVA, A. and TSIMILLI-MICHAEL, M. (2000): The fluorescence transient as a tool to characterize and screen photosynthetic samples. In: M. Yunus, U. Pathre, P. Mohanty (eds.): *Probing Photosynthesis: Mechanism, Regulation and Adaptation*. Taylor and Francis, UK, Chapter 25, pp. 445–483.
- SUNOJ, V.S.J., WEN, Y., JAJOO, A., SHORT, A.W., ZENG, W.H., ELSHEERY, N.I. and CAO, K.F. (2023): Moderate photoinhibition of PSII and oxidation of P700 contribute to chilling tolerance of tropical tree species in subtropics of China. *Photosynthetica*, 61(SPECIAL ISSUE 2023/1): 177-189. doi: 10.32615/ps.2022.039
- TERASHIMA, I., FUNAYAMA, S. and SONOIKE, K. (1994): The site of photoinhibition in leaves of *Cucumis sativus* L. at low temperatures is photosystem I, not photosystem II. *Planta*, 193: 300-306. doi: 10.1007/BF00192544
- TIETZ, S., HALL, C.C., CRUZ, J.A. and KRAMER, D.M. (2017): NPQ(T): A chlorophyll fluorescence parameter for rapid estimation and imaging of non-photochemical quenching of excitons in photosystem-II-associated antenna complexes. *Plant, Cell & Environment*, 40(8): 1243-1255. doi: 10.1111/pce.12924
- VIRTANEN, O., KHOROBRYKH, S. and TYYSTJÄRVI, E. (2021): Acclimation of *Chlamydomonas reinhardtii* to extremely strong light. *Photosynthesis Research*, 147(1): 91-106. doi: 10.1007/s11120-020-00802-2
- WOODFORD, R., WATKINS, J., MOORE, M., NIX, S., YEE, S., CHAN, K. X., POGSON, B., CAEMMERER, S., FURBANK, R. and ERMAKOVA, M. (2024/2025 – preprint): PGR5 promotes energy-dependent non-photochemical quenching to enable efficient C₄ photosynthesis under fluctuating light. *bioRxiv*. doi: 10.1101/2024.09.15.613160; <https://www.biorxiv.org/content/10.1101/2024.09.15.613160v1.full>