Responses of primary photosynthetic processes to repetitive rehydration differ in two representatives of Svalbard moss flora

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Abstract

Global warming in polar regions brings a risk of more frequent and long-lasting dry periods due to warmer and windier climate during polar summers. Mosses are well adapted to desiccation-rehydration events and they have evolved remarkable constitutive and inducible mechanisms of desiccation tolerance. In our study, *Sanionia uncinata* and *Racomitrium lanuginosum* were collected in Svalbard and used for laboratory-based repetitive 32-h-lasting rehydration cycles with continuous monitoring of restoration of their primary photosynthetic processes measured by chlorophyll fluorescence parameters. Immediately after the addition of water to dry thalli, potential quantum yield of PSII (F_V/F_M) was about 50% of its maximum reached after 32 h of rehydration. In a course of time of rehydration, both species showed an increase in F_V/F_M and effective quantum yield (Φ_{PSII}) following a S-curve relationship. Non-photochemical quenching did not show clear trend with the rehydration time, It differed between the two species and showed both decrease and increase with the time of rehydration. Relative chlorophyll fluorescence decrease (RFd), which is considered a vitality indicator, increase with the time of rehydration showing similar trends in the first and the third cycle of rehydration. The results indicate that both *Sanionia uncinata* and *Racomitrium lanuginosum* are resistant to desiccation since F_V/F_M and Φ_{PSII} recovered fully after 32 h of rehydration and there we only minor differences in the two parameters between the first and third rehydration cycle.

Key words: Svalbard, dehydration, rehydration, chlorophyll fluorescence, *Sanionia uncinata, Racomitrium lanuginosum*

Symbols and abbreviations: ChlF – chlorophyll fluorescence, KK – slow Kautsky kinetics of chlorophyll fluorescence, F_V/F_M – potential yield of photochemical photosynthetic processes in PSII, Φ_{PSII} – effective yield of photochemical photosynthetic processes in PSII, NPQ – non-photochemical quenching of chlorophyll fluorescence, F_S – steady-state fluorescence

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Introduction

Polar regions and regions with cold climates are characterized by extreme environmental conditions, where mosses experience constant stress, including sub-zero temperature, high radiation and water availability - frequent cycles of hydration and dehydration during vegetation period (Bramley-Alves et al. 2015). At the same time, mosses are capable to quickly return to normal life upon rehydration (Proctor et Smirnoff 2000, Alpert 2000, Wood 2007, Bhatt et al. 2020, Orekhova et al. 2022). The restoration of vital activity depends on the speed, duration and other conditions of drying / rehydration (Hinshiri and Proctor 1971, Green et al. 2011, Stark et al. 2013). In addition, the restoration of photosynthetic function is species-specific (Proctor et al. 2007, Nabe et al. 2007, Zhang et al. 2011, Nayaka and Saxena 2014, Orekhova et al. 2022).

Plants in polar region are changing at a more alarming rate than anticipated. There is well documented greening in the Arctic as ice retreats exposing more land. Research shows that this region is amongst the most rapidly warming on the planet (*e.g.* [1]-IPCC 2019, Wawrzyniak and Osuch 2020). The climate in the area of the Hornsund station is warming more than 6 times faster than the global average (+0.17°C per decade). It reflects the positive trend of mean annual temperature in the last four decades ([2]-NOAA 2020). Warmer temperature and increasing melt promote plant growth, however some plants in subpolar and polar regions may suffer from lack of water available during spring and summer season. The research conducted so far has shown that mosses from polar regions are at risk of drying and dying due to windier summers caused by ozone depletion and climate change (Robinson et al. 2020). In this context, research on physiological limits of drier mosses is significant since it may not only contribute to national and international science and recent state-of-art in stress physiology of mosses, but may provide guidelines for future protective measures for polar vegetation.

Bryophytes are frequently subjected to cyclic desiccation-rehydration events and they have evolved remarkable constitutive and inducible mechanisms of desiccation tolerance (Li et al. 2014). The process of drying and rehydration can be repeated several times without causing major changes in the functioning of the organism (Stoklasa-Wojtasz et al. 2012). Many studies (*e.g.* Proctor et al. 2007, Oliver et al. 2009, Pressel and Duckett 2010, Fernández-Marín et al. 2011, Stark et al. 2013, Hu et al. 2016, Zhang 2016, Pizarro et al. 2019, Orekhova et al. 2022) have focused on desiccation tolerance and adjustment of photosynthesis to different thallus hydration ranging from fully wet to dry state.

Studies focused on moss desiccation tolerance/resistance usually use photosynthetic parameters as markers (for review *see* Morales-Sánchez et al. 2022). Usually, they combine several different methods, especially gasometric and chlorophyll fluorescence. Tuba et al. (1996) measured the RFd vitality parameter (relative decrease in fluorescence – Haitz and Lichtenthaler 1988) simultaneously with the measurements of gas exchange in the moss *Tortula ruralis* ssp., exposed to desiccation-rehydration cycles. The approach of using exclusively chlorophyll fluorescence parameters to evaluate interspecific differences in mosses exhibiting varying degrees of desiccation resistance has been performed as well (Csintalan et al. 1999, Bartošková et al. 1999, Nabe et al. 2007).

The aim of our study was to evaluate chlorophyll fluorescence parameters in two selected moss species from Svalbard during rehydration. A set of experiments was performed on the two model moss species exposed to several cycles of laboratory-induced dehydration / rehydration.

Attention was paid in particular to the physiological responses of chloroplast photosynthetic apparatus, especially functioning of photosystem II under drying. The effects of repeated cycles of hydration and dehydration on PSII functioning were evaluated as well and key underlying protective mechanisms identified. Acclimation of mosses, their PSII in particular, to repeated cycles, if there is any, were identified at the level of chlorophyll fluorescence parameters (F_V/F_M, Φ_{PSII}, and NPQ). Where appropriate, the objective is to distinguish the components of non-photochemical quenching, as affected by manipulated dehydration/rehydration.

Material and Methods

Sample collection and handling

For the experiments focused on ecophysiology of photosynthesis, moss samples were collected in Svalbard (Fig. 1). For the purpose, *Sanionia uncinata* and *Racomitrium lanuginosum* were selected, since they are dominant species in Svalbard (*Sanionia*: Virtanen et al. 1997, Uchida et al. 2002). These species were collected from the neighbourhood of the Polish research station (Hornsund, Svalbard, *see* Fig. 2 and Table 1) during summer season of 2021. The collection and handling, including the drying of samples and transport to Europe, were done by Polish staff (Włodzimierz Sielski and Joanna Perchaluk).
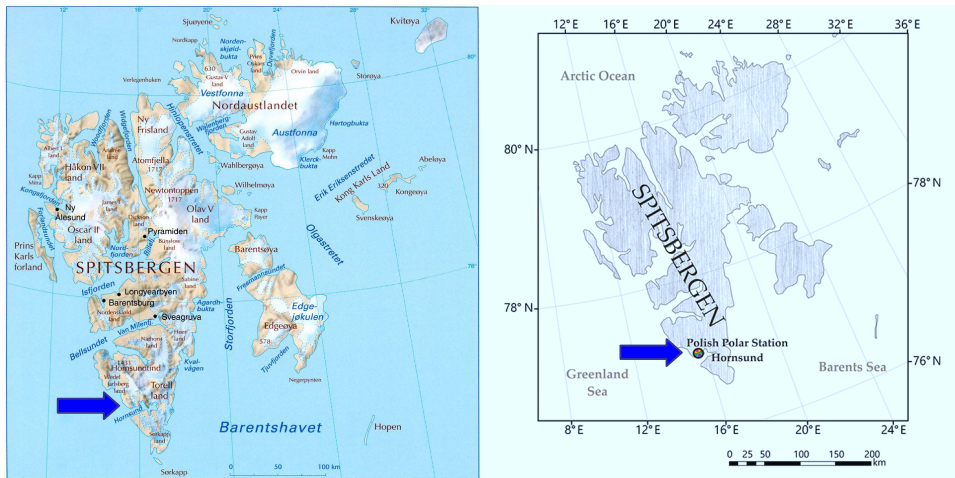
Fig. 1. Map of Svalbard with indication of the collection sites (Wawrzyniak and Osuch 2020). For the source of the maps, *see* the Web sources [3-Map of Svalbard].

Sanionia uncinata   *Racomitrium lanuginosum*

Fig. 2. Photographs of experimental moss species: *Sanionia uncinata* (left), and *Racomitrium lanuginosum* (right). Dry and wet specimens are presented.

Chlorophyll fluorescence parameters during desiccation

After the transfer of moss samples to the Masaryk university, Brno (Czech Republic), the experiments included rewetting studies (32 h, sample temperature: 5°C, light: 10 µmol m^{-2} s^{-1} PAR) with the evaluation of primary photosynthesis as restored after rehydration. Time courses of effective quantum yield of PSII (Φ_{PSII}) as dependent on time of rehydration were constructed and interspecific differences identified. Second set of experiment included the evaluation of dehydration re-

sponse curves of photochemical photosynthetic processes as reflected in the following chlorophyll fluorescence parameters: steady-state chlorophyll fluorescence (F_S), effective quantum yield of photochemical processes in photosystem II (Φ_{PSII}), and non-photochemical quenching of absorbed light energy (NPQ). For calculation of Chlorophyll fluorescence decrease ratio (RFd) we used the formula suggested by Lichtenthaler et al. (1986): RFd = $(F_M - F_S) / F_S$ since it is considered to be a proxy of photosynthetic CO_2 exchange. Flexas et al. (2002) and Lichtenthaler et al. (2005) demonstrated the RFd was well correlated with CO_2 fixation.

| Species	Number of samples	Date of collection	Coordinates
Sanionia uncinata	1	30.07.2021	77°00.423'N 15°32.848'E
	2	05.08.2021	77°00.430'N 15°32.817'E
	3	05.08.2021	77°00.445'N 15°32.808'E
Racomitrium lanuginosum	4	05.08.2021	77°00.244'N 15°32.043'E
	5	05.08.2021	77°00.254'N 15°33.078'E
	6	05.08.2021	77°00.275'N 15°33.165'E

Table 1. Geographical coordinates of sampling location *S. uncinata* and *R. lanuginosum* close to the Hornsund station.


Results

Reactivation of photosynthesis during rehydration

Samples of *S. uncinata* and *R. lanuginosum* underwent 3 consecutive rehydration-dehydration cycles. Majority of chlorophyll fluorescence parameters had similar time courses in the first and second cycle of rehydration. Therefore, only the data for the first and third cycles are presented. Figs. 3 and 4 show the slow Kautsky kinetics (KKs; normalized to background chlorophyll fluorescence F_0) recorded during the first and third cycle of thallus rehydration. The shape of KKs of chlorophyll fluorescence differed species-specifically and with time of rehydration, similarly to the evidence reported by Giudici et al. (2018) for partly and fully wet moss species. Both species showed flattened KKs in the third cycle of rehydration (compared to the first cycle) and lower values of peak chlorophyll fluorescence F_P. Time of rehydration changed the KKs in both species. Immediately after water addition, KKs were flat and showed generally low chlorophyll fluorescence values. Then, after a 30 min. rehydration, chlorophyll fluorescence increased which was demonstrated by higher values than those recorded immediately after water addition. Rehydration of 24 and 32 h led to a decrease of chlorophyll fluorescence signal followed by an increase and gradually increased F_M values that reached their maximum after the 32 h rehydration. The same was true for F_M' values which were found the highest in both species after the 32 h rehydration in the first and the third cycle as well. In KKs, *S. uncinata* showed less distinguishable F_P point in the third cycle than in the first cycle of dehydration (*see* the arrows in Figs. 3 and 4).
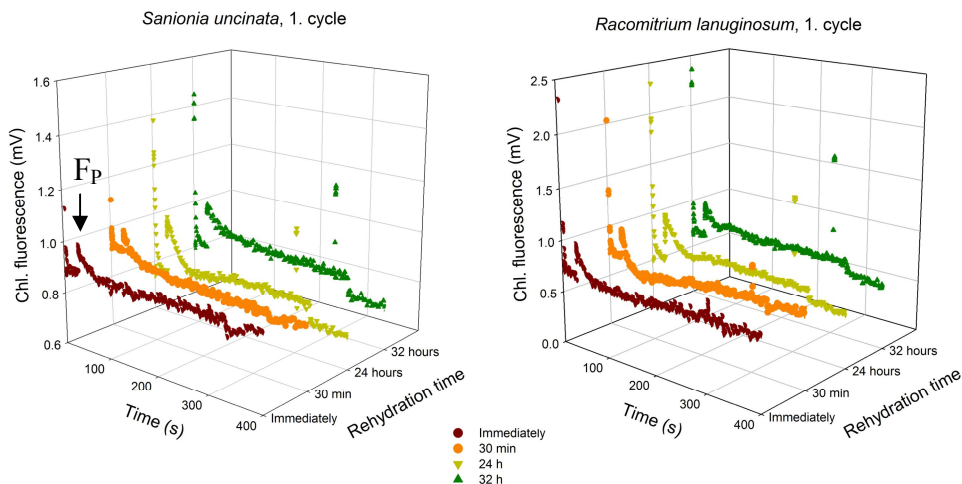
Fig. 3. Slow Kautsky kinetics curves (KKs) recorded during 32h-lasting rehydration from dry to wet state in *Sanionia uncinata* (left) and *Racomitrium lanuginosum* (right) – 1st cycle of rehydration. F_P indicates the peak chlorophyll fluorescence reached immediately after the exposition of a sample to continuous light.
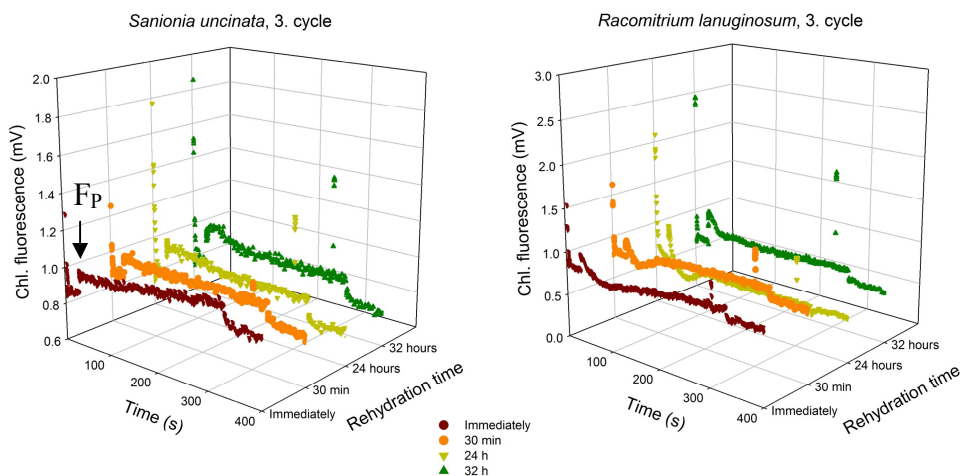
Fig. 4. Slow Kautsky kinetics curves (KKs) recorded during 32h-lasting rehydration from dry to wet state in *Sanionia uncinata* (left) and *Racomitrium lanuginosum* (right) – 3rd cycle of rehydration. F_P indicates the peak chlorophyll fluorescence reached immediately after the exposition of a sample to continuous light.

Rehydration response curves of chlorophyll fluorescence parameters showed the time required for complete restoration of primary photosynthetic processes in PSII. For both species, 24 h was the time to reach maximum values of F_V/F_M and Φ_{PSII} (Figs. 5 and 6) for the first and the third rehydration cycle, respectively.

For *R. lanuginosum*, a gradual increase in NPQ was observed in the first cycle, whereas in the third cycle of rehydration, the curve shows a complex polyphasic character with an increase in values up to 24 h, followed by a linear decrease by 32 h. The response of NPQ to repetitive rehydration cycles did not show a clear trend. It needs more data to analyze the protective mechanisms involved in NPQ. Rehydration-response courses of NPQ were found species-specific. In *S. uncinata*, non-photochemical quenching (NPQ) showed almost unchanged values during the rehydration in the first cycle, and a slight decrease in the third cycle. In both species, NPQ values showed lower val-

ues in the third cycle of rehydration then in the first one with an exception found in *R. lanuginosum* after 24 h of rehydration (NPQ higher in the third than in the first cycle) followed by gradual decline with the time of rehydration towards the first cycle NPQ values. Absolute values of NPQ, however, were found much larger in *R. lanuginosum* than *S. uncinata* in the first and the third cycle of rehydration.

RFd values exhibited an increasing trend with the time of rehydration. However, the difference between the first and the third cycle during the whole rehydration period was both positive and negative, irregularly distributed over the rehydration time.
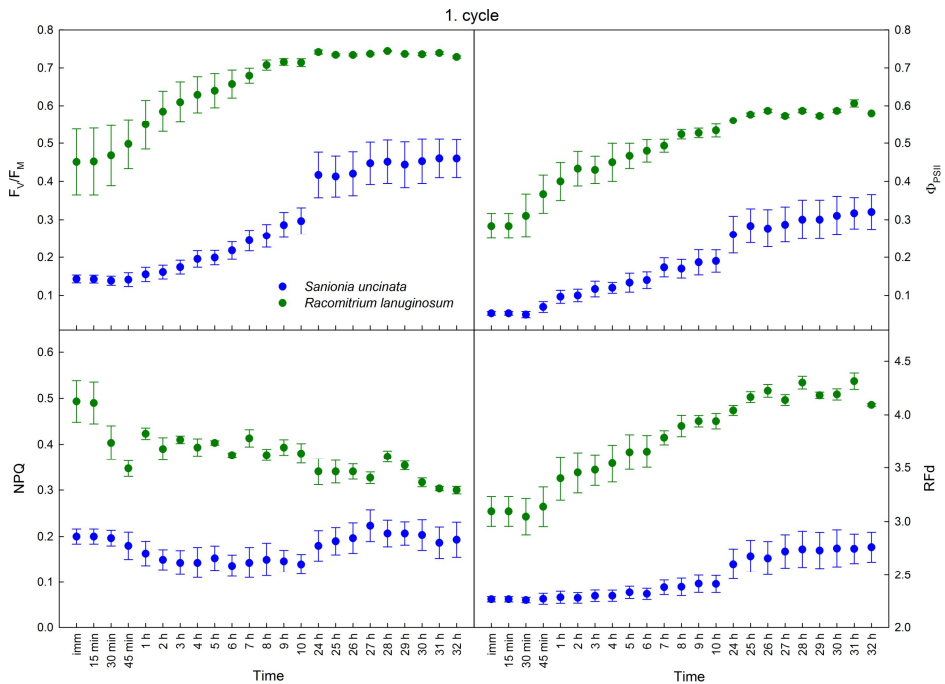

Fig. 5. Chlorophyll fluorescence parameters recorded during the 1st cycle of rehydration. Data points represent means of 5 replicates. Error bars are ± standard deviations.
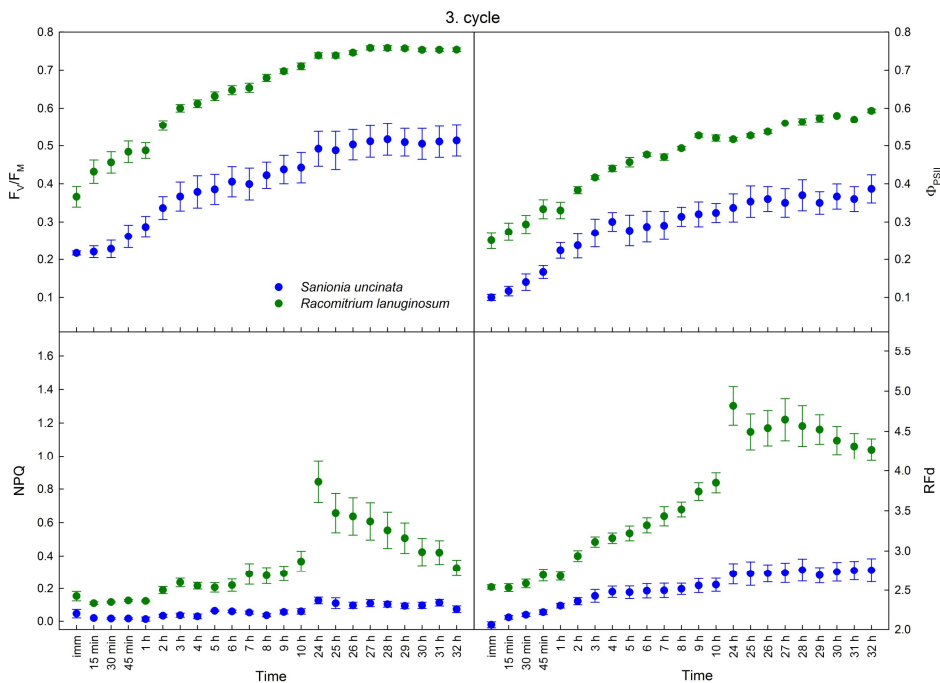
Fig. 6. Chlorophyll fluorescence parameters recorded during the 3rd cycle of rehydration. Data points represent means of 5 replicates. Error bars are ± standard deviations.

In general, the differences in chlorophyll fluorescence paramaters related to the cycle of rehydration were species-specific. The differences in F_V/F_M and Φ_{PSII} between the first and the third cycle of rehydration are shown in Fig. 7. While F_V/F_M and Φ_{PSII} in *S. uncinata* showed an increase followed by a decrease of the difference, *R. lanuginosum* exhibited close-to-zero difference throughout the time of rehydration. Therefore, the difference between the cycles was found in *S. uncinata* exclusively.
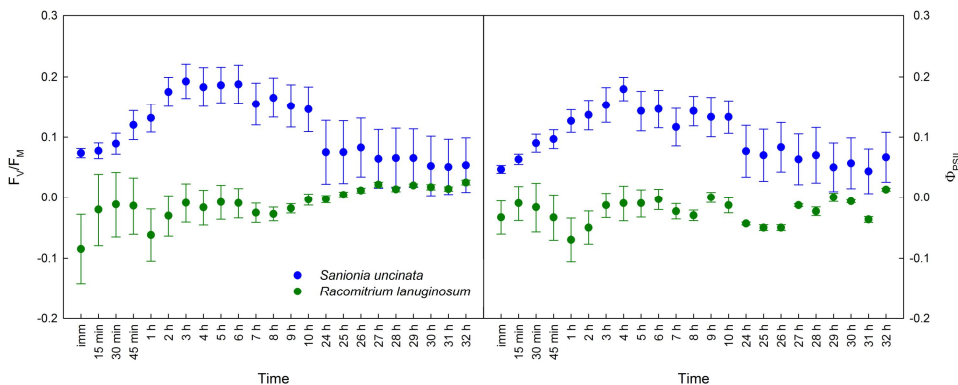
Fig. 7. The difference in F_V/F_M and Φ_{PSII} values found between the first and the third cycle of rehydration. The difference ($\Delta F_V/F_M$, $\Delta \Phi_{PSII}$) was calculated as the third – the first cycle values.

Discussion

Rehydration of moss thallus can occur within few minutes, however, the recovery of cellular functions and photosynthetic parameters related to PSII (*see* Figs. 5 and 6) is a longer process taking few hours (Csintalan et al. 1999). Several authors have reported species-specific rehydration time (evaluated typically by F_V/F_M): 1 h (Proctor et al. 2007), 16 h (Csintalan et al. 1999), 20 h (Nabe et al. 2007), 25 h (Nayaka and Saxena 2014). These species-specific differences can be attributed in particular to the length of the previous period of physiological activity in a hydrated state. Green et al. (2011) reported rapid restoration of photosynthetic processes in moss from stone surfaces (rapid and repetitive hydration/dehydration). In contrast, mosses that were wet for a long time before drying, needed a longer time to restore their photosynthetic processes (Stark et al. 2013). Our data showed that 24 h was the time long enough to restore photosynthetic capacity (*see* F_V/F_M in Figs. 5, 6) in both experimental species.

Since the two Arctic mosses used in our study undergo a relatively rapid drying in the field (due to the joint action of wind speed and temperature), the time of rehydration found in our study (32 h) might be attributed to their ecophysiological strategy related to location. In this concept, the desiccation tolerance of both types of mosses is related to the rate of dehydration. A recent study by Pizarro et al. (2019) found that about 40 h was sufficient to restore the effectiveness of PSII in rehydrated *Sanionia uncinata* from King George Island, Antarctica. Other studies from non polar regions report even shorter period of about 11 h as sufficient to restore primary processes of photosynthesis associated with PSII (Greenwood et al. 2019 for *Bryum argenteum*).

Our data indicate that a repeated dehydration lead to some short-term acclimatory changes. While repeated rehydration caused an increase in F_V/F_M and Φ_{PSII}, (in 3rd cycle of rehydration, relative to the 1st rehydration) in *S. uncinata*, the rehydration response curves of F_V/F_M and Φ_{PSII} were almost same in *R. lanuginosum*. This may suggest that with repeated rehydration, PSII functioning performs better in *S. uncinata* than *R. lanuginosum*. Such short-term acclimatory change may represent an advantage for *S. uncinata* at the sites with frequent dehydration / rehydration events. This idea might be supported by the fact that *S. uncinata* showed lower NPQ values in the third rehydration cycle (compared to the 1st one) while the NPQ behavior in *R. lanuginosum* was rather unclear (*cf* 1st and 3rd cycle of rehydration). Anyway, NPQ increase in rehydrated mosses might be associated with the activity of quenching centres which are formed during desiccation in mosses (Heber et al. 2007). Underlying mechanism of the quenching centres formation is desiccation-induced alteration in the conformation of a specific pigment–protein complex. The formation of the quenching centres is considered reversible.

The effects of repeated dehydration / rehydration cycles varies in mosses according to the environmental conditions, water availability in particular. Davey (1997) showed that hydric species suffered greater loss of photosynthesis during repeated cycles. In contrast, greater recovery in mesic and xeric mosses was observed from repeated cycles. Moss species from polar regions might be ranked among those which cope well with repeated rehydration / dehydration cycles (Pizarro et al. 2019). For follow up studies focused on the effects of repeated rehydration / dehydration cycles, a multidisciplinary approach covering chlorophyll fluorescence, relative water content, content of photosynthetic pigments, osmolytes, phytohormones and sugars, proteome analysis, gene expression, reactive oxygen species, and enzymatic ac-

tivity measurements are recommended, because the response of moss species is complex (for review *see* Morales-Sánchez et al. 2022).

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