

Photoprotective mechanisms activated in Antarctic moss *Chorisodontium aciphyllum* during desiccation

Kumud Bandhu Mishra^{1,2*}, Miroslav Rosputinský², Matúš Griesš², Anton Puhovkin^{2,3,4}

¹Laboratory of Ecological Plant Physiology, Global Change Research Institute, Czech Academy of Science, Bělidla 4a, 603 00 Brno, Czech Republic

²Laboratory of Photosynthetic Processes, Department Experimental Biology, Faculty of Science, Masaryk University, Kamenice 5, 62500 Brno Czech Republic

³State Institution, National Antarctic Scientific Centre, Ministry of Education and Science of Ukraine, Taras Shevchenko Blvd. 16, Kyiv 01601, Ukraine

⁴Institute for Problems of Cryobiology and Cryomedicine, National Academy of Science of Ukraine, Pereyaslavska Str. 23, Kharkiv 61016, Ukraine

Abstract

We investigated the relationship between relative water content (RWC) of Antarctic moss *Chorisodontium aciphyllum* and several chlorophyll fluorescence parameters evaluating primary photochemical processes of photosynthesis. During the gradual dehydration of *Ch. aciphyllum* from fully wet (RWC=100%) to dry (RWC=0%) state, progression of NPQ (non-photochemical quenching) induction curves were recorded; the maximum NPQ (NPQ_{max}) attained at the end of illumination period (10 min.), and NPQ relaxation in dark were all analysed. Induction curves of photosynthetic electron transport rate (ETR) were also evaluated, as well as two parameters, ETR_{max} and initial slope, were derived from the curve: (1) ETR_{max}; (2) initial slope (α parameter). The two parameters were related to the degree of desiccation (RWC declining from 100 to 0%). It was found that NPQ induction curves and the parameters derived from them were sensitive to dehydration and may be used as markers for dehydration-induced changes in photosystem II functioning of desiccating *Ch. aciphyllum*. The activation of non-photochemical quenching during desiccation and the underlying mechanisms are discussed.

Key words: non-photochemical quenching, NPQ induction, Antarctica, Galindez Island, Argentine Islands

DOI: 10.5817/CPR2024-1-1

Introduction

Water relations in mosses

Mosses and lichens are poikilohydric plants and they dominate the flora of the polar regions. While both species frequently coexist, lichens tend to predominate in dry environments like deserts, whilst bryophytes tend to predominate in humid habi-

Received January 16, 2024, accepted July 15, 2024.

*Corresponding author: K. B. Mishra <mishra.k@czechglobe.cz>

Acknowledgements: KBM thanks to the Czech Science Foundation (project number 22-29315S; LM2023048). The other authors thank the infrastructure of the CARP (Czech Antarctic Research Program) for providing the facilities of the Extreme Environments Life Laboratory (Department of Experimental Biology, Masaryk University, Brno) and support of the experimental work. The authors thank the Czech Antarctic Infrastructure (CARI) for providing laboratory facilities for the experiments reported in this study. The author (AP) is grateful to the Ukrainian State Targeted Programme of Research in the Antarctic for 2011–2025. AP thanks every defender of Ukraine whose work allowed him to implement this research.

tats such as rainforests (Green and Lange 1995). They are indeed dominant components of vegetation oases in Antarctica. Davey *et al.* (1997) reported that water, not temperature, is the most important factor limiting moss photosynthesis in Antarctic coastal regions.

Depending on air humidity and the availability of water, Antarctic mosses react quickly to variations in the availability of liquid water. When there is a shortage of water, they respond immediately by drying out, which is followed by a gradual decline in photosynthetic activity (Robinson *et al.* 2000, Kappen and Schroeter 2002). Drying off the mosses thallus has an adverse impact on both primary and secondary photosynthetic processes. How-

ever, the rate of net photosynthesis of Antarctic mosses cells may be reduced with high water content (Robinson *et al.* 2000) due to the phenomenon of water supersaturation of the thallus and the accompanying reduced diffusion of CO₂ molecules into intrathalline space (Tuba *et al.* 1996). The degree of stress tolerance of moss species, in particular, to supersaturation by water and their photosynthetic performance is species-specific. Wasley *et al.* (2006) reported that *Grimmia antarctici* has a comparatively high tolerance to water immersion and a relatively low tolerance to desiccation. *Ceratodon purpureus*, on the other hand, had a reasonably high tolerance to desiccation but a relatively low tolerance to water immersion.

Dehydration resistance of mosses in respect to photosynthetic processes

Mosses, in general, are resistant to dehydration and inhibit their photosynthetic processes when they lose substantial amount of water from their thalli. Orekhova *et al.* (2022a) studied the inhibition of primary photosynthetic processes in two Antarctic mosses (*Brachythecium austroglareosum* and *Bryum pseudotriquetrum*) in desiccating thalli. They found that effective quantum yield of PS II photochemistry (Φ_{PSII}) remained unchanged within relative water content (RWC) decrease from fully wet (100%) to semidry (30%); below 20% RWC, Φ_{PSII} was declined but it showed a species-specific response. A half-decrease in Φ_{PSII} was reached at an RWC of 12.6% in *B. austroglareosum* and 9.8% in *B. pseudotriquetrum*. These findings showed that primary photosynthetic processes, in these two mosses, exhibited a high degree of desiccation resistance in order to survive in the harsh Antarctic environment.

In the field, however, resistance of moss photosynthetic processes to desiccation depends on co-acting environmental factors, *e.g.*, period of dryness, tempera-

ture and irradiance during desiccation, as well as number of dehydration/rehydration cycles that a particular moss species underwent (Green *et al.* 2011, Orekhova 2022b). On dehydration, the PSII reaction center activity is lost in a manner similar to photosynthetic CO₂ fixation, whereas the PSI reaction center remain active in some desiccation-tolerant bryophytes. PSII fluorescence was also quenched in dried mosses and lichens. Although reductions of PSII fluorescence in dried lichens were attributed to decreased fluorescence efficiency due to preferential energy distribution to PSII. The quenching, according to Bilger *et al.* (1989), is caused by an interruption of energy transfer from light-harvesting Chl *a/b* protein complexes of PSII (LHCII) to PSI core complexes in dry lichens. But in dry mosses, it was proposed that Chl720, a reaction center Chl dimer of PSII, can be produced from P680 to quench PSII fluorescence (Heber and Shvalov 2005). Therefore, there is ongoing debate regarding the reason behind the desiccation-induced quenching of PSII fluorescence.

Non-photochemical quenching in desiccating mosses

Non-photochemical quenching (NPQ) is a highly complex photoprotective mechanism in photosynthetic organisms that dynamically modulates the dissipation of excess light into heat while preserving and protecting the electron transport flow. Photosynthetic systems thereby avoid photo-oxidative stress and photoinhibition. The components of NPQ have variable induction and relaxation kinetics: the fastest (1-2 min.) and most rapidly reversible kind, qE, is dependent on a trans-thylakoid pH induced by excess light which protonates particular residues on pH sensitive trigger protein PsbS. In many photosynthetic organisms, an additional NPQ component, well known as state transition component, qT (half time 5-10 min.), is produced as a result of the phosphorylation-induced displacement of LHCII from PSII to PSI. Photoinhibitory quenching (qI, with half life time hours) is the slowest component and includes components from the slow and reversible inactivation of photosystem II (PSII) reaction centers as well as other long-term processes involved in light acclimation. In bryophytes species, NPQ phenomena were suggested to be important in

avoiding photoinhibition under drying conditions.

NPQ induction curves are typically used in the studies focused on *Arabidopsis* mutants having different structure of PSII and LHC (e.g. Li et al. 2004, Dikaios et al. 2019) and altered capability to cope with a high light stress (Takahashi et al. 2009). In lichens and mosses, few attempts have been made to use this method to quantify interspecific differences in NPQ processes (e.g. Mkize et al. 2022), or photoinhibition sensitivity (Barták et al. 2023). In our study, we examined the hypothesis that NPQ induction curves might be utilised effectively to access the desiccation-induced changes in functioning of photosynthetic apparatus in mosses. Therefore, we focused on the change in shape of the NPQ induction curves during desiccation of *Chorisodontium aciphyllum* thalli, variations in maximum NPQ and the rate of dark recovery of NPQ values. We expected that these parameters would be related to the photosynthetic electron transport rate (ETR) evaluated using the chlorophyll fluorescence technique.

Material and Methods

Experimental species and sample collection

Chorisodontium aciphyllum is a common moss in both the sub-and maritime Antarctica. The range of the species covers southern South America, the Falkland Islands, the Scotia Arc, the Antarctic Peninsula and associated islands, Tristan da Cunha, Amsterdam Island, and the Kerguelen archipelago (for details see Hyvönen 1991, Ochyra et al. 2008, and references therein).

Ch. aciphyllum was collected near the Ukrainian Antarctic Station Akademik Vernadsky on Galindez Island (Argentine Is-

lands), West Antarctica, during the summer seasonal Antarctic expeditions in 2022-2023. The collection site was a moss bank Smith located in a close vicinity of the station (see Fig. 1). After collection, the vigorous, brightly fresh moss (15 x 15 cm) was dried out naturally in a shaded area close to the station before being transported to the laboratories to the Czech republic in a portable fridge. In the laboratories, the sample was kept in a refrigerator at 5°C. Before experiment, subsamples (4 cm²) were immersed in demineralized

water (bottom part, *i.e.* dead lower thallus parts) and hydrated for 48 h by regular spraying (upper part with green leaves). For the experiments, most vigorous sub-

samples were selected, *i.e.*, those exhibiting the highest F_V/F_M values (measured on 5-min. predarkened material by a PAM-2000 fluorometer – data not shown).

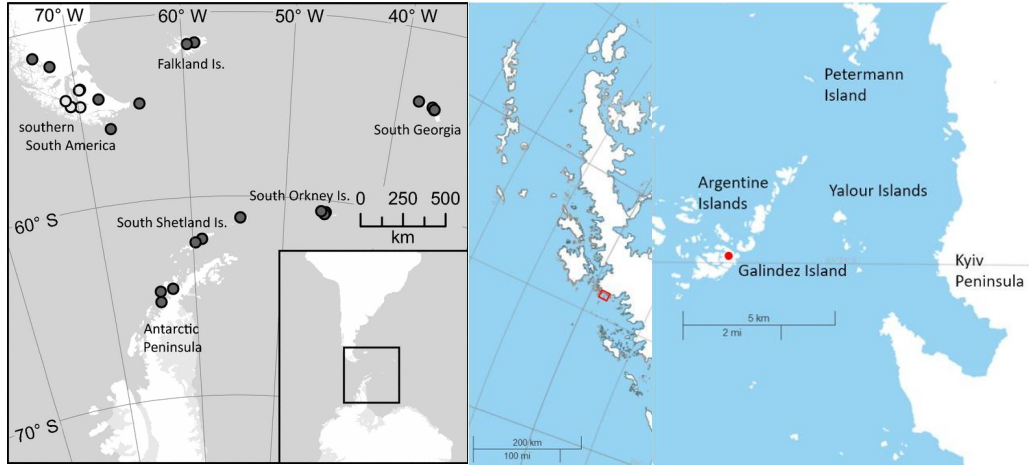


Fig. 1. Left: *Chorisodontium aciphyllum* range (indicated by circles) in Southern America, Falkland Island, South Georgia, South Orkneys, South Shetlands (*source*: Biersma *et al.* (2018)). Right: Site of samples collection at Galindez Island.

Chlorophyll fluorescence measurements

Chlorophyll fluorescence parameters of *Ch. aciphyllum* thalli were measured by a PAM 2500 fluorimeter (Walz, Effeltrich, Germany). After 10 min. dark adaptation, the induction curves of non-photochemical quenching (NPQ) of thalli's were measured. The advantage of the method is that a curvilinear (exponential) increase in NPQ was recorded while exposure to a constant actinic light. In our experiment, we exposed *Ch. aciphyllum* thalli to $100 \mu\text{mol}$ (photons) $\text{m}^{-2} \text{s}^{-1}$ of photosynthetically active radiation for 400 s. During this light period, a saturation pulse was applied every 60 s to induce maximum chlorophyll fluorescence signal (F_M')

which allowed to calculate the Φ_{PSII} , ETR, and NPQ using the equations below.

The actinic light was then switched off for 180 s (dark period), and saturation pulses were applied every 20 s in order to measure maximum saturation pulse-induced chlorophyll fluorescence and, consequently, calculated NPQ values during dark-relaxation period. The ETR values recorded during the light period of the measurement were plotted against the illumination period. From the curves, the maximum values (ETR_{max}) and the slope of the relationship (α parameter) were calculated using the in-built formulas in the PAM-2500 fluorometer.

Results

In a fully hydrated state (RWC = 100%), NPQ induction curves showed a gradual increase in NPQ values during the light period, reaching its maximum after 5 min. of illumination and remained constant thereafter; during dark relaxation period, NPQ decreased to 50-60% of its maximum (see Fig. 2). In partially dehydrated state, thalli of *Ch. aciphyllum* exhibited a rapid increase to maximum values (at 60 s of illumination time), followed by an exponential decrease to a constant value found at the end of the illumination period (see Fig. 2). Except for fully hydrated thalli, the maximum NPQ value of thalli with other specific RWCs decreased, and this trend

became more pronounced as thallus dehydration progressed. During the dark relaxation period, NPQ values decreased exponentially. In extremely desiccated thalli (e.g., 30% RWC), reduction in NPQ induced actinic light after one minute of exposition was substantially faster than in control (RWC=100%). NPQ values exhibited much smaller decrease immediately after the light was switched off. However, during dark-relaxation, the NPQ values showed a gradual curvilinear increase with duration of darkness. This was in contrast with the dark relaxation kinetics of NPQ commonly observed in higher RWCs of *Ch. aciphyllum* thalli.

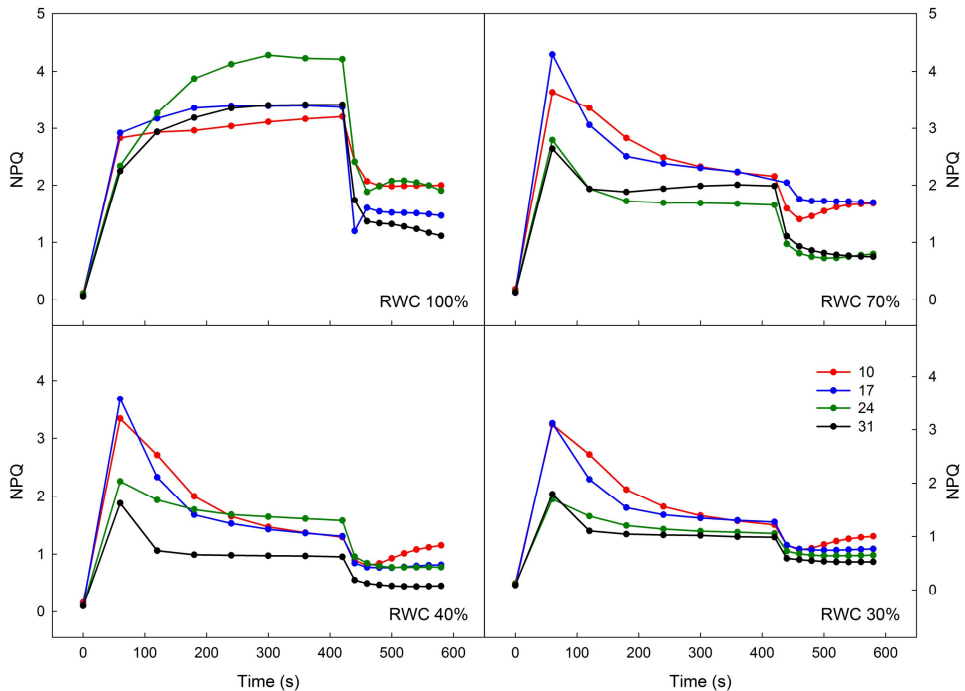


Fig. 2. Changes in shape of NPQ induction curve with progressive desiccation of *Ch. aciphyllum* thalli (from 100 to 18% of relative water content: RWC) .

The shape of the ETR curves in response to illumination time was found to be dependent on RWC. While fully hydrated *Ch. aciphyllum* thalli (RWC=100%)

had ETR_{max} of about 30, it increased with partial dehydration to the values of 50-60 found within the RWC range decreasing from 70 to 40%. With severe thallus dehy-

dration, a decrease in ETR_{max} values appeared (*see* ETR_{max} of about 14 found for thalli desiccated to 18% of RWC – Fig. 3). Apart of ETR_{max} , the slope of the ETR curves (alpha parameter, α) exhibited desiccation-induced change. Two different responses were identified in the measured samples. One group showed a gradual in-

crease in alpha parameter with desiccation (Fig. 4, right), while the second group showed an increase with thallus dehydration from RWC of 100 to 50-60%, where the alpha parameter was maximum. Then, after dehydration, α dropped to about half of its maximum value.

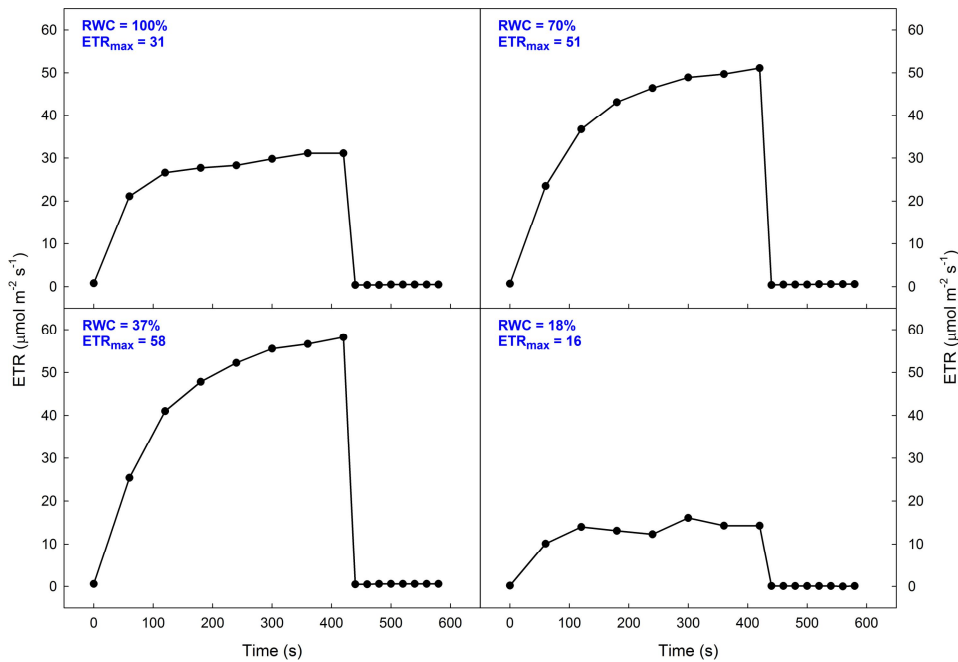


Fig. 3. Time courses of photosynthetic electron transport rate ($\mu\text{mol (electrons) m}^{-2} \text{s}^{-1}$) in *Ch. aciphyllum* were recorded in desiccating thalli with a decreasing relative water content (RWC).

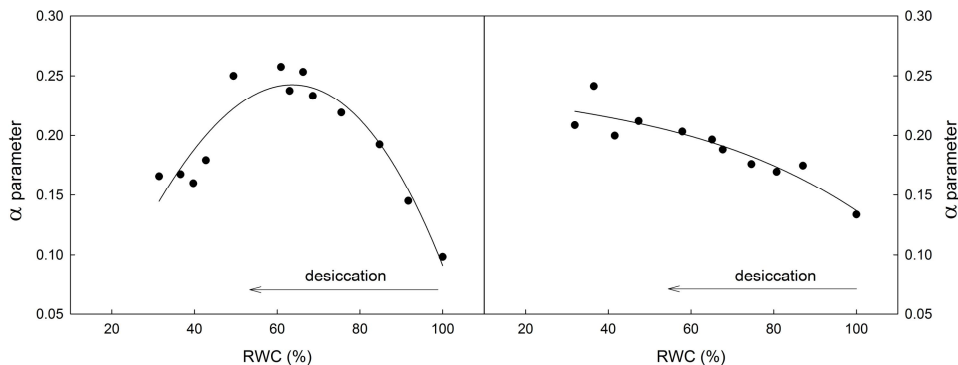


Fig. 4. Correlation between the slope of ETR curves (alpha parameter) and *Ch. aciphyllum* desiccation recorded for two subgroups of thalli.

Discussion

All oxygenic photosynthetic organisms have evolved photoprotective mechanisms known as NPQ, which causes thermal dissipation of excitation energy absorbed beyond the capacity of downstream metabolic reactions. Chlorophyll fluorescence, which is used to assess NPQ, is challenging to interpret in bryophytes due to the overlapping NPQ mechanism. When exposed to high irradiance, photosynthetic organisms develop the ability to convert between quenching states, which allow them to safely release excess obtained energy via heat. The fastest dissipative NPQ reaction represented by qE is triggered with protonation in thylakoid membrane initiated with low pH, followed by a change from state II to state I as LHCII deattaches from PSII and shifts towards PSI and vice versa, and finally by quenching due to photoinhibition. Here, we observed that NPQ induction curves either (1) exhibited a typical shape in fully-hydrated state, *i.e.* curvilinear increase during the light period (*see e.g.* Beckett et al. 2021), or (2) exhibited an early peak of NPQ, achieved immediately after the start of illumination, followed by a gradual NPQ reduction with further illumination, as shown in Fig. 2. The two distinct shapes of NPQ time courses may be recorded even under the same conditions for two distinct clades of same species as demonstrated by Permann et al. (2022) for *Zygnema* ssp. In algae, Berteotti et al. (2015) described a polyphasic behaviour of NPQ induction during the illumination phased in WT *Chlamydomonas reinhardtii*. Pierangelini et al. (2019) observed the phenomenon of transient relaxation of NPQ during the illumination period and they attributed the fast occurrence of oxidation of the PQ pool and the movement of the light-harvesting complex II from PSI to PSII, *i.e.* state II to I transition (Roach and Na 2017).

Medium to severe drought stress in desiccating moss thalli typically results in reduced emission of the overall chlorophyll fluorescence signal, as indicated by a dehydration-induced drop in steady state chlorophyll fluorescence (F_S). The decline of F_S in mosses, at RWC under 40%, was reported by several authors (*e.g.* Giudici et al. 2018, Orekhova 2022a). This decline is thought to be caused by an increase in non-photochemical quenching that occurs with desiccation. Yamakawa and Itoh (2013) state that this type of quenching in poikilohydric plants is exclusively caused by dryness referred to as d-NPQ, in contrast to that induced by high light (abbreviated l-NPQ). In our experiment, dominant share of d-NPQ from the total NPQ could be expected because the desiccation occurred under low light conditions. However, an interaction between d-NPQ and l-NPQ could be expected during final phases of thallus dehydration. Under those settings, even low light may cause light-induced NPQ. Some poikilohydric plants maintain photosynthetic activity during dehydration processes until approximately 90% of free water in the cells is depleted (Nabe et al. 2007). Recently, three distinct mechanisms of NPQ activation during desiccation of mosses have been examined (Yamakawa et al. 2012, for review *see* Sánchez et al. 2022).

Our findings suggest that activation of NPQ was highly effective in desiccating *Ch. aciphyllum* thalli because the NPQ recorded at the end of illumination time was more or less constant (NPQ about 2) throughout the RWC declining from 70 to 40% (Fig. 2), and ETR_{max} was substantially high ranging from 51-59 (Fig. 3). Then, as RWC fell below 20%, NPQ (derived from the induction curve) and ETR values decreased rapidly, indicating severe limitations in primary photochemical reactions of

photosynthesis as well as protective mechanisms. Our findings demonstrated that the technique of NPQ induction curves might

be used in photosynthetic research in poikilohydric autotrophs during desiccation.

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