Desiccation resistence of photosynthetic processes in photosystem II of Antarctic moss *Sanionia uncinata* assessed by two chlorophyll fluorescence methods

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Abstract

Dehydration-induced decrease of photosynthetic performance in mosses is a general response to thallus dessication. The decrease is caused by changes in photosystem II (PSII) functioning which is sensitively reflected in several chlorophyll fluorescence (ChlF) parameters. Apart from the decrease in potential yield of photosynthetic reactions in PSII (F_V/F_M), several protective mechanisms are activated during moss desiccation, non-photochemical quenching (NPQ) in particular. This is study focused on NPQ changes during the desiccation of Antarctic moss *Sanionia uncinata*. NPQ induction and relaxation curves were recorded during gradual dehydration from a fully wet state (relative water content [RWC] = 100%) to a fully dry state (RWC = 0%). Three key NPQ parameters were evaluated: NPQ_{max} (maximum value), NPQ_{termin} (at the end of induction) and NPQ_{relax} (end of dark relaxation). The initial slope (α) and dark relaxation (β) of NPQ were analysed. Additionally, fast chlorophyll fluorescence transients (OJIPs) were measured and the parameters related to PSII functioning evaluated for decreasing RWC. The relationships between the ChlF parameters and RWC were investigated. Results indicated that NPQ induction and relaxation curves – along with the OJIP-derived parameters were sensitive to dehydration. Since critical RWC for all the investigated ChlF parameters were found below 20%, *Sanionia uncinata* might be ranked into drought-resistant moss species.

Key words: fast chlorophyll fluorescence transient, OJIP, non-photochemical quenching, NPQ induction/relaxation, James Ross Island, Antarctica

DOI: 10.5817/CPR2025-1-10

Received June 3, 2025, *accepted* September 10, 2025.

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Acknowledgements: The authors are grateful for the oportunity to use CARP infrastructure and the facilities of Antarctic research (CZ.02.1.01/0.0/0.0/16_013/0001708, CEP: EF16_013/0001708).

Introduction

Mosses are poikilohydric autotrophs showing high desiccation tolerance. They are capable to cope with variable periods of desiccation/rehydration cycles and restore their photosynthetic acticity when rehydrated (Perera-Castro and Flexas 2022). Desiccation tolerance is defined as the ability of an organism to recover normal physiological function upon rehydration after experiencing a desiccated state, characterized by a minimum water potential of −100 MPa, returning to a fully hydrated state (water potential 0 MPa). In moss-vegetated areas in maritime Antarctica, desiccation tolerance of Antarctic mosses has become increasingly relevant due to an observed warming trend of Antarctic vegetation oases. Recent ongoing climate change in Antarctic coastal vegetation oases with moss cover brings both an increase in productivity, abundance, and cover due to increased water availability in maritime Antarctica (Wierzgoń et al. 2023), and limitation of physiologically active time during austral summer season due to drier environment in continental Antarctica (Colesie et al. 2023). The latter change is driven by high air temperature, low relative air humidity, and low availability of liquid water (Perera-Castro et al. 2020, 2021).

Methods based on chlorophyll fluorescence represent an effective tool in studying the desiccation resistence in Antarctic mosses both in field- (Schroeter et al. 2017, 2021) and laboratory-based (Robinson et al. 2000) studies. Several chlorophyll fluorescence parameters are widely employed in the evaluation of desiccation-induced stress in chloroplasts of poikilohydric autotrophic organisms. Potential (F_V/F_M) and effective quantum yields (Φ_{PSII}) are frequently applied to quantify limitations in primary photosynthesis. F_V/F_M is defined as the maximal quantum efficiency of photosystem II. This parameter serves as an indicator of sustained stress and estimation of physiological recovery in desiccation tolerance experiments (Csintalan et al. 1999, Proctor 2001, Perera-Castro et al. 2021, Ríos-Meléndez et al. 2021). The effective quantum yield (Φ_{PSII}), defined as light-adapted efficiency of photosynthetic processes in PSII (Schreiber and Bilger 1987, Murchie and Lawson 2013), is often estimated in mosses to evaluate the desiccation-induced decline in PSII and overal photosynthesis (Giudici et al. 2018, Orekhova et al. 2022).

It is well established that moss desiccation leads to activation of physiological mechanisms in order to protect photosystem II from overenergization and negative effects of reactive oxygen species (ROS) formation (Salih et al. 2024). At the early stage of drought stress in mosses, inducion the enzymatic and non-enzymatic scavenging systems happens in order to sequester ROS (Zhang et al. 2017).The mechanism involves an enhancement of non-photosynthetic pathways of absorbed light energy dissipation, demonstrated by increase in non-photochemical quenching of chlorophyll fluorescence (Nabe et al. 2007). Such mechanism protects PSII of desiccating mosses from overenergization and are typically fully reversible upon rehydration (Yamakawa and Itoh 2013). Desiccation typically leads to ROS formation. Consequent oxidative stress leads to inactivation and oxidative destruction of PSII core. Such responses to desiccation at chloroplast level are associated with antioxidative enzymes production and activity in desiccating mosses (*e.g.* Bansal and Shrivastava 2017, Morales-Sánchez et al. 2022). In the field, desiccation-induced limitation in PSII effectivity is accompanied by ligh-induced stress to PSII, *i.e.* phenomenon of photoinhibition in Antarctic mosses (Schlensog et al. 2003), and lichens (ul Haq et al. 2024). However, studies focussed on co-action of the two factors in mosses are almost missing (*e.g.* Nabe et al. 2007).

Non-photochemical quenching(NPQ) includes three components: energy-dependent quenching (qE), state-transition quenching (qT) and photoinhibitory quenching (qI) (Müller et al. 2001). The first two components relax rapidly upon return to non-stressed conditions, whereas qI recovers slowly (over hours to days) and is the primary component affected by desiccation stress. Morover, activation of thermal energy dissipation mechanisms protects the photosynthetic machinery of bryophytes against photo-oxidative damage during dry state (Bilger 2014). The above-specified protective mechanisms co-act during desiccation of poikilohydric mosses and form overall non-photochemical quenching (NPQ) which sensitively reflects desiccation changes in poikilohydric autotrophs. Typically, NPQ increases in response to desiccation stress in mosses (Proctor 2001, 2010). Recently, a new method of NPQ induction/relaxation has been introduced to plant stress physiology, to evaluate desiccation-induced changes in NPQ and decline in PSII functioning. The shape of the NPQ induction and relaxation curves is affected by stress factors and differs from the control. This approach allows for the rapid testing of plants under desiccation stress since the induction part of the curve (recorded on light) differs according to intrethalline relative water contents (Mishra et al. 2024). Moreover, slow rate of NPQ dark relaxation after desiccation also implies that photosynthetic activity remains lower than optimum found in hydrated thali (Beckett et al. 2005 for lichens). In consequence, desiccation-induced non-photochemical quenching plays an important role in desiccation tolerance, with implications on timing of physiological responses. Therefore, it needs to be considered when outlining experimental protocols.

Fast chlorophyll fluorescence transients (OJIPs) have been used in mosses to evaluate the response of PSII to a variety of stressors, including thallus dehydration (Bartošková et al. 1999, Giudici 2021). With progressive moss desiccation, gradual loss of chlorophyll fluorescence is reported which is reflected both in flattening of the OJIP curve (lower values of chlorophyll fluorescence) and a decrease in the OJIP-derived parameters related to PSII functioning (ET_0/RC – photosynthetic electron transport per PSII reaction centre, PI_{ABS}/RC – performance index sensu Strasser et al. 2004). The proces is reversible and an increase in chlorophyll fluorescence values as well as an increase in photosynthetic electron transport is apparent uppon rehydration of dry thalli (Bhatt et al. 2019). The OJIP approach was used to evaluate the photoinhibition effects in wet thalli of Antarctic moss species *Sanionia uncianta* from east and west of the Antarctic peninsula (Orekhova et al. 2021).

In our study, we combined two approaches of chlorophyll fluorescence (fast chlorophyll fluorescence transient – OJIP, and non-photochemical quenching induction/relaxation curves) in order to evaluate desiccation tolerance, changes in PSII functioning and protective mechanisms in chloroplast, non-photochemical quenching in particular in Antarctic moss *Sanionia uncinata*. We hypothesized that particular photosynthetic and protective mechanisms will be high since the species is considered highly desiccation-tolerant. On the other hand, we expected that the activation of protective mechanisms will have different extent during gradual desiccation. Therefore, the aim of this study was to evaluate desiccation tolerance of the species by applying the two below-specified approaches: (1) evaluation of relative water content in *S. uncinata,* at which the most remarkable negative changes to PSII functioning happens, and (2) indication of particular processes inhibited in PSII at different degrees of thallus desiccation.

Material and Methods

Collection site / Species characteristics

Sanionia uncinata was collected at the James Ross Island, Antarctica (Fig. 1), by Davide Giordano, a member of the Czech Antarctic Expedition to Mendel station in the austral summer season of 2005 (January-March). Moss samples were collected from vegetation oases (Paradise valley: 63.495203 S, 57.492440 W) in wet state (Fig. 2). After collection, they were dried under natural conditions in a shaded place outside the Mendel station and then transferred to Europe in dry state. In last decade, several studies focused various aspects of *S. uncinata* ecophysiology (Naktsubo et al. 2002, Orekhova and Hájek 2022, Choi et al. 2022, de Vargas et al. 2024).

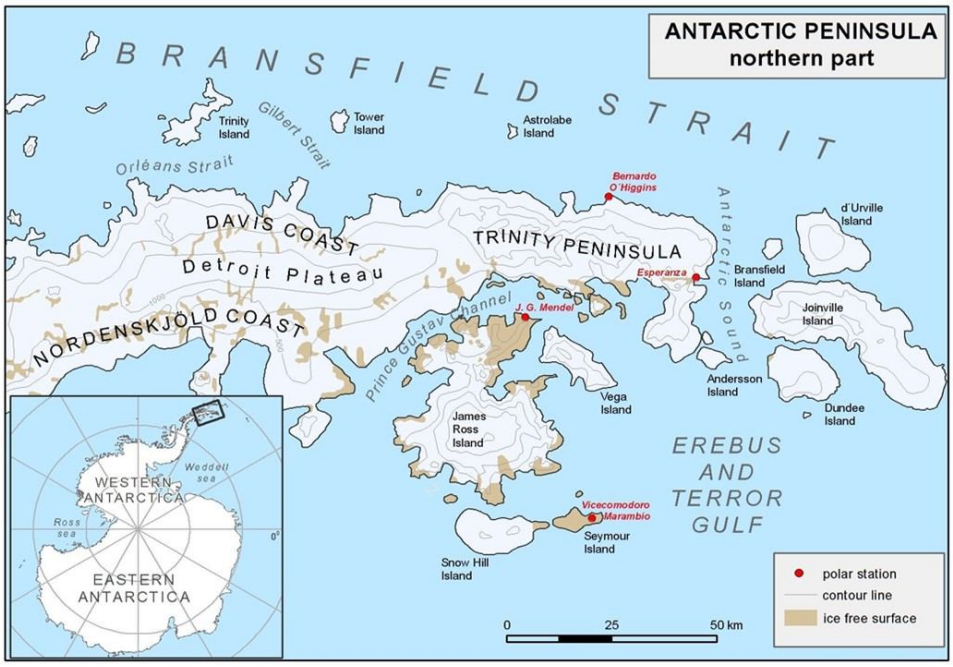

Fig. 1. Map of the Antarctic Peninsula, and James Ross Island with indication of *Sanionia uncinata* collection site (blue dot). Modified from source map (Stachoň et al. 2014).

The species is quite abundant in maritime Antarctica, especially along the western coast of the Antarctic Peninsula (Hedenäs 2012). It has been investigated in the field in polar regions and in a laboratory-based experiments in numerous studies focused on photosynthesis (*e.g.* Ueno et al. 2006, Orekhova et al. 2021), and the following aspect of moss biology: intrathalline carbohydrate content (Zúñiga-González 2016), content of biologically-active compounds (Ivanova et al. 2007, Theodoro et al. 2024), potential to absorb air pollutants (Kolon et al. 2020, Samecka-Cymerman et al. 2011), and last but not least, desiccation-induced synthesis of enzymatic antioxidants and expression of late embryogenesis abundant (LEA) proteins (Pizarro et al. 2019).

Fig. 2. Collection site is a moss-dominated vegetation oasis with abundant *Bryum pseudotriquetrum* (freshly green), and *Sanionia uncinata* (yellowish green). General view (left), a detail of collection spot (right). Photo (credit) Davide Giordano.

NPQ induction/relaxation curves

Non-photochemical quenching induction/relaxation curves of *Sanionia uncinata* thalli were measured by a PAM 2500 fluorometer (Walz, Effeltrich, Germany) in fully hydrated thalli (48 h rewetting in a fridge, 5°C) first, and then at different degrees of desication at laboratory temperature. Moss sampes (typically 1.8 cm^2 of green thalli) desiccated naturally in a special holder allowing gradual desiccation. Before each chlorophyll fluorescence measurements, fresh weight of samples were measured on laboratory scales in order to allow calculation of relative water content (RWC) at which the measurement was taken:

$$RWC = (FWDD - DW) * 100 / (FWo - DW),$$

where FWDD is the FW of the sample recorded at any time during the desiccation period, DW is the DW of the sample and FWo is the initial FW at the beginning of the experiment.

Samples were provided 15 min. dark adaptation and then exposed to continuous light of 700 μmol m^{-2} s^{-1}, of photosynthetically active radiation (PAR) for 4 min. During this light period, saturation pulses of high light (2 000 μmol m^{-2} s^{-1} for 1.5 s) were applied every 30 s to induce maximum chlorophyll fluorescence signal (F_M') which allowed to calculate the Φ_{PSII}, ETR, and NPQ using the following equations:

$$\Phi_{PSII} = (F_M' - F_S) / F_S$$

$$ETR = (PAR * 0.84 * \Phi_{PSII}) / 2$$

$$NPQ = (F_M - F_M') / F_M'$$

where F_M is the maximum chlorophyll

fluorescence reached after saturation pulse (SP) applied in the dark-adapted state, F_M' is the maximum chlorophyll fluorescence reached after an SP is applied in the light-adapted state (at the end of the light period), F_S is the chlorophyll fluorescence recorded at the end of the light period and PAR is the photosynthetically active radiation.

Then, the light was then switched off and moss samples recovered in dark for the period of 3 min. During the dark period, saturation pulses were applied every 20 s in order to measure maximum saturation pulse-induced chlorophyll fluorescence and, consequently, evaluate NPQ values during dark-relaxation period. The ETR values recorded during the light period of the measurement were plotted against the light period. From the ETR curves, the maximum values (ETR_{max}) were calculated using the in-built formulas in the PAM-2500 fluorometer.

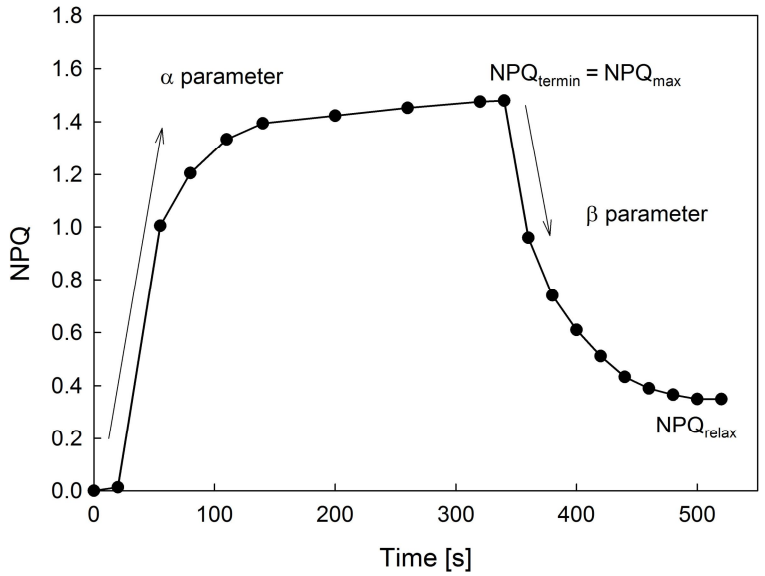

Fig. 3. Typical NPQ induction curve with definitions of the parameters used in the study: NPQ recorded at the end of NPQ induction (light period), *i.e.* the terminal value of NPQ (here equal to maximum value), α parameter – the slope of the initial part of NPQ induction, β parameter – the slope of the initial NPQ decrease at the beginning of the dark period (relaxation curve). The α and β parameters are calculated as ΔNPQ/Δtime(s).

The relationships of NPQ to RWC were calculated for descending RWC classes (80%–100%, 60%–80%, 40%–60%, 20%–40%, and 0%–20%).

From the NPQ curves for particular RWC class, the following parameters were calculated: (1) the initial slope of NPQ increase at the beginning of the actinic light period (α), (2) the ratio of decrease (NPQ_{max} – NPQ_{relax}) / NPQ_{relax}, (3) the slope of the initial decrease at the beginning of the dark relaxation period (β), and (4) NPQ_{relax}.

OJIP analysis

To evaluate the effect of *S. uncinata* thallus desiccation on PSII functioning, fast kinetics OJIP were recorded during gradual desiccation by a PAR-FluorPen portable fluorometer (Photon Systems Instruments, Drásov, Czech Republic). Samples were dark adapted for 15 min. using the fluorometer leaf-clips, then a polyphasic rise of chlorophyll fluorescence was induced by the exposition of sample to a saturating light pulse of 3 000 μmol (photons) m^{-2} s^{-1} for 2 s and stored in the instrument memory using the fluorometer's OJIP protocol. OJIP-derived chlorophyll fluorescence parameters (for the list, *see* Supplementary Materials) were calculated using the formulae by Strasser et al. (2004). And plotted against RWC in order to evaluate the effect of thallus desiccation on particular PSII-related process.

Statistical analysis

The effects of desiccation (expressed as RWC) on chlorophyll fluorescence parameters were evaluated through a one-way ANOVA using the STATISTICA software with $P = 0.05$.

Results

In a fully hydrated state (RWC = 80–100%), the NPQ induction curve showed a gradual increase in NPQ values during the light period of measurement, reaching a maximum at the end of light period (*see* Fig. 4). The value of NPQ_{max}, however, did not represent absolute maximum, since the NPQ values still showed a rising trend at the end of light period. The same was valid for the RWC classes 60–80%, and 40–60%. Moreover, the shape of the NPQ induction curve was, as well as NPQ_{max}, almost same for the three RWC classes indicating that at the end of light period non-photochemical quenching mechanisms were activated to same extent. The difference was found, however, for alpha parameter which increased with desiccation suggesting faster involvement of protective mechanisms forming NPQ in the first minute upon illumination. With more severe desiccation, *i.e.* in the RWC classes of 20–40%, and 0–20%, NPQ induction curve decreased in values showing a phenomenon of flattening the NPQ induction curves (for more details, *see* Discussion).

During the dark relaxation period, NPQ values decreased exponentially for all evaluated RWC classes. The expoonential decrease, however, was more pronounced in initial and moderate phase of thallus dehydration (RWC decrease from 100 to 40%). With severe thallus desiccation, *i.e.* at the RWC class of 20–40%, only slight relaxation of NPQ values was observed, *i.e.* the decrease from NPQ_{max} to NPQ_{relax}. Apart from the RWC-dependent differences in relaxation of NPQ values, the speed of the NPQ decrease (beta parameter) was found desiccation-dependent. The initial rate of NPQ decrease at the very beginning of the dark period was highest at the RWC class 80–100%, and decreased as the RWC decreased. The relative decrease in NPQ during the relaxation period gradually diminished as the degree of desiccation increased with declining RWC classes. The most apparent change in the relative decrease of NPQ in dark period was found in the RWC classes 20–40%, and 0–20% (Fig. 5).

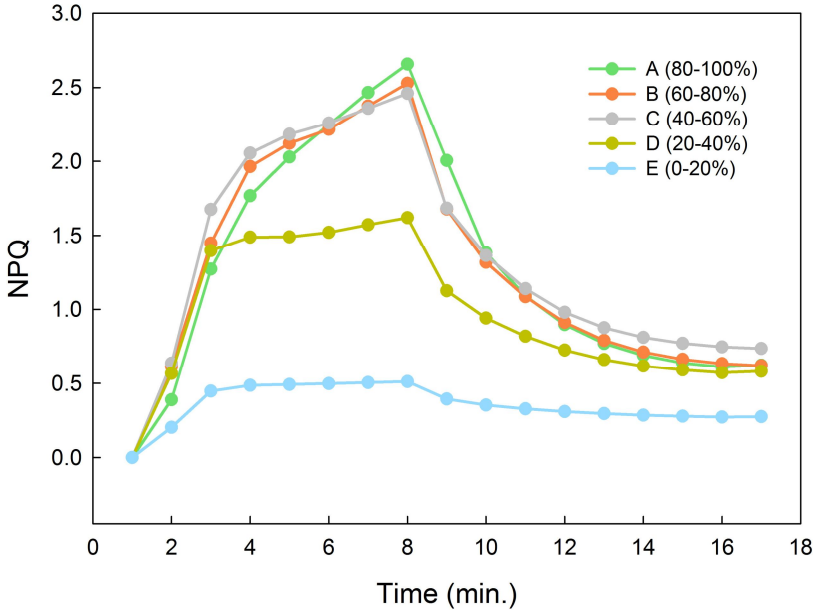

Fig. 4. NPQ induction/relaxation curves recorded in desiccating *Sanionia uncinata* for classes of relative water content (RWC): A: 80–100% (green line), B: 60–80% (orange line), C: 40–60% (grey line), D: 20–40% (yellow line), and E: 0–20% (blue line). Data points are means of 10 replicates, standard deviation (not indicated) is below 15% of means.

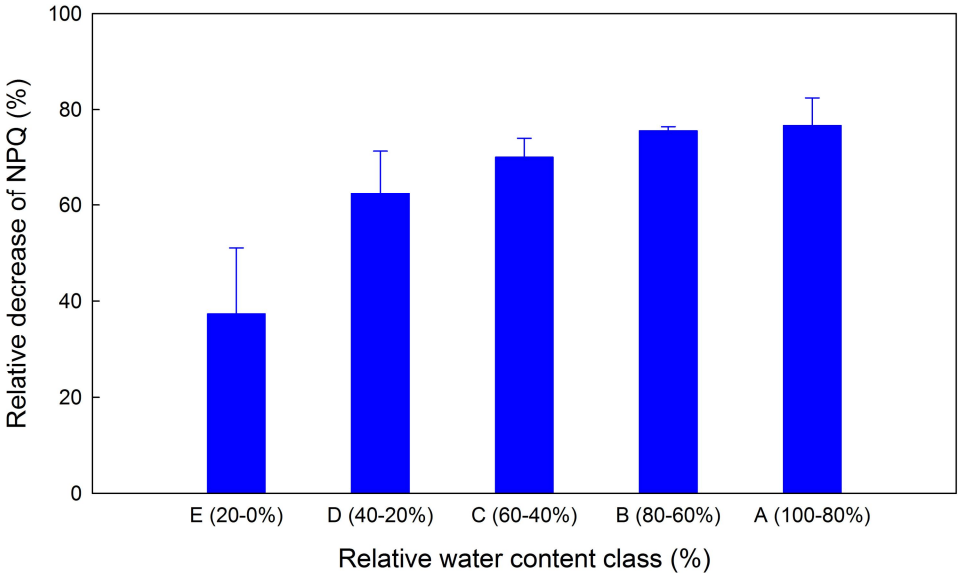

Fig. 5. Relative decline of NPQ recorded for dark period (relaxation from NPQ_{max} to $NPQ_{terminal}$) as dependent on relative water content (RWC) in *Sanionia uncinata* thalli. Bars represent mean values calculated from 10 replicates. Error bars indicate standard deviations. RWC classes are A: 80–100% , B: 60–80% , C: 40–60% , D: 20–40% , and E: 0–20%.

Desiccating thalli of *Sanionia uncinata* showed a decrease in chlorophyll fluorescence values forming an OJIP curve, a phenomenon known as a "flattening" of the OJIP curve with the decreasing RWC (*see* Fig. 6). Most severe desiccation-induced decrease in chlorophyll fluorescence was found for the RWC class 0–20%. When normalized to F_P (data not shown here), desiccation dependent increase in relative chlorophyll fluorescence at J, and I point was found (compared to F_P) which indicated negative effect of desiccation on electron flow throug Q_a-Q_b, and hydroxy plastoquinone pool (for more details, *see* Discussion.

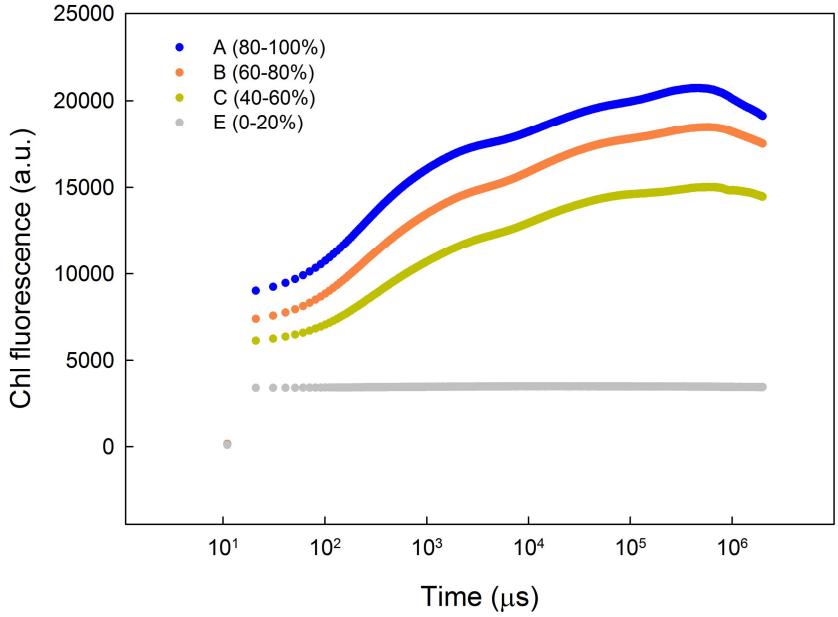

Fig. 6. Fast chlorophyll fluorescence transients of *Sanionia uncinata* as recorded for desiccation classes of relative water contents (RWC): (A) 80–100% (blue symbols), (B) 60–80% (orange symbols), (C) 40–60%, (E) 0–20% (yellow symbols).

OJIP-derived parameters responded to RWC decrease sensitively reflecting a desiccation-induced reduction in PSII functioning (Fig. 7). F_V/F_M declined with progressive dehydration from the RWC around 40% to a dry state (RWC = 0%). Maximum F_V/F_M values were found at hydrated state (RWC = 40–100%). At full hydration, slightly lower F_V/F_M was found indicating the phenomenon of suprasaturation by water (*see* Discussion). During thallus desiccation, F_V/F_M remained almost unchanged within a wide range of RWC (100–40%) and then declined sharply to the values close to 0. Such behavious indicates desiccation resistence of poikilohydric autotrops. Severe desiccation (*i.e.* RWC under 20%) caused a decrease in the performance index (PI_{ABS}), photosynthetic electron transport per reaction centre (ET_0/RC), as well as and trapping rate per RC (TR_0/RC). Protective mechanism were activated during severe thallus desication (RWC 0–20%) which led to an increase in thermal dissipation per RC (DI_0/RC), and absorption per RC (ABS/RC).

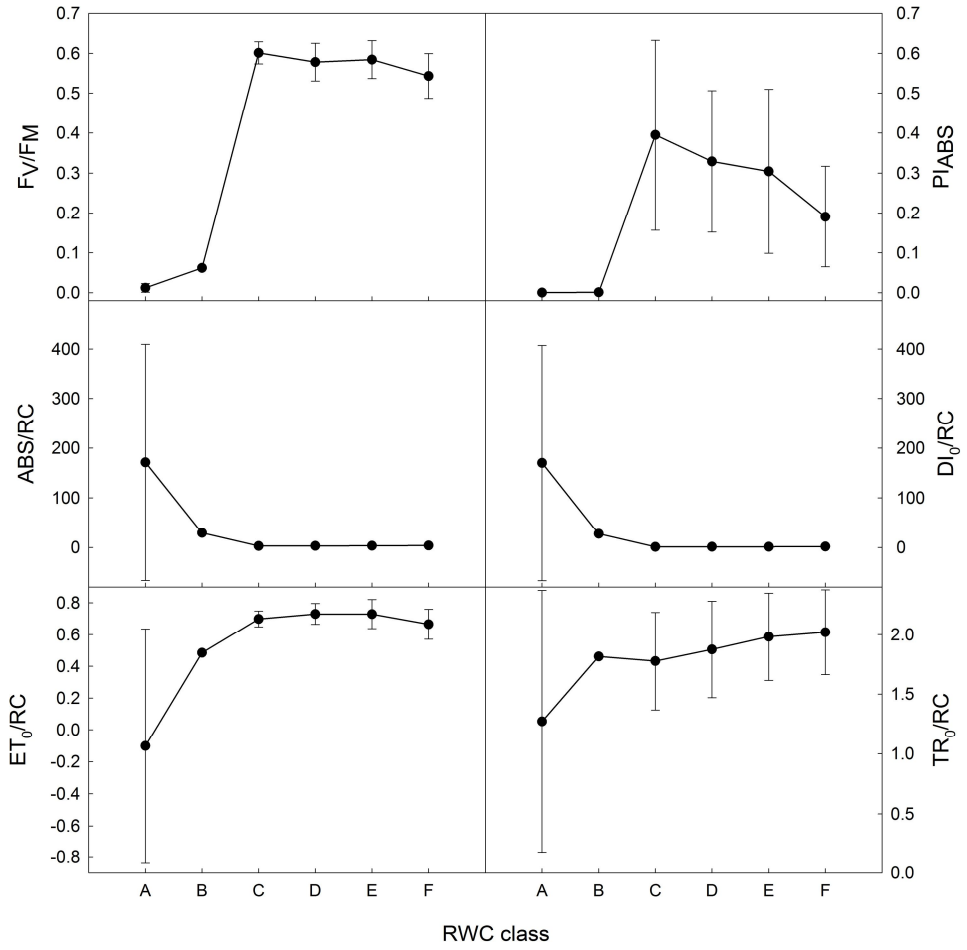

Fig. 7. OJIP-derived parameters in *Sanionia uncinata* as recorded for desiccation classes of relative water contents (RWC). *Note*: F (Full hydration, RWC = 90–100%), A (RWC = 0–20%).

Discussion

The shape of the NPQ induction curves was found desiccation-dependent. When considering the shape of NPQ induction in fully hydrated or close to fully hydrated autotrophs, the following three options reported by Beckett et al. (2021) and reviewed by Hájek et al. (2025, MS under review) can be distiguished: (1) a gradual increase in NPQ with a maximum constant value found at the end of the light period, (2) a rapid increase in NPQ with the maximum value reached before the end of the light period, followed by a slight decrease, and (3) a gradual increase with a rise in NPQ that had not reached a plateau at the end of the light period. Recently, a model (analytical pipeline system) has been proposed by Ramakers et al. (2025) to analyse NPQ induction kinetics taking into account intensity of PAR intensity. The authors reported that at low PAR, the (1) shape is typically achieved, (below 200 μmol (pho-

tons) m^{-2} s^{-1}). When PAR is over 400 μmol (photons) m^{-2} s^{-1}, NPQ induction, the (2) NPQ increased during the whole light period (10 min. in the study of Ramakers et al. 2025). Our data presented in Fig. 3 well correspond to this situation.

As desiccation progressed, the NPQ induction curves changed, showing lower absolute NPQ values as thallus RWC declined below 40% and lower values. This observation is supported by the study of Mishra et al. (2024), who measured the NPQ induction curve in Antarctic moss *Chorisodontium aciphyllum*. The NPQ values at the end of the light period decreased with thallus desiccation. However, the authors reported a change in the NPQ induction curve shape, with an increase at the beginning of the light period, followed by a decline towards the end, similar to category. This type of change in shape was not observed in our data for *S. uncinata*.

The initial slope of the NPQ induction curves (α) showed an increase in the decreasing RWC classes until the RWC of 40–60% was reached. This pattern suggest faster activation of NPQ within the first second of illumination is comparable to data presented by Mishra et al. (2024), who observed a gradual increase throughout the desiccation period (RWC declining from 100%). However, the same study showed that the desiccation-induced increase in α could be followed by a decrease when RWC fell below 50%. The initial rate of NPQ dark relaxation (β parameter) changed with RWC. It became less steep, indicating negative desiccation-induced changes to PSII functioning as RWC declined. This finding aligns with evidence from other stressors that limit the dark relaxation of NPQ, such as high temperature (Permann et al. 2022), high light-induced photoinhibition of PSII (Kress and Jahns 2017), and UV-B stress (Xue et al. 2022). Recently, the effect of Chl *b* deprivation in a moss mutant (*Physcomitrium patens*) NPQ induction/relaxation curve, including the β parameter change is reported (Zhang et al. 2023). Therefore, both α and β changes, as affected by desiccation in the species involved in our study, indicate the negative effects of desiccation and suggest they could be used as indicators of drought stress in mosses.

Analysis of the NPQ induction/relaxation curves showed that the parameters derived in this study may serve, alongside traditional ChlF (either those derived from OJIPs or those derived from slow Kautsky kinetics of chlorophyll fluorescence recorded for different degrees of thallus desiccation, *see* e.g. Giudici (2021), as indication of desiccation stress. The analysis of NPQ induction/relaxation curves provides an insight into protective mechanisms activated during initial phase and declining at severe phase of thallus desiccation.

In our study, F_V/F_M declined with RWC decrease in a similar manner that was reported for desiccating moss *Racomitrium subsecundum* (Nayaka and Saxena 2014) having a critical RWC at which PSII photosynthetic processes are fully inhibited at the RWC of 5–10%. Typically, fast desiccation-induced decline in F_V/F_M values is accompanied by increased dissipated heat as indicated by the simultaneous increase of thermal dissipation of absorbed excitation energy, DI_0/RC (*see* Fig. 6). This reported for other stressors as well, *e.g.* by Orekhova et al. (2021) for a photoinhibition-induced increase in DI_0/RC in *S. uncinata*. In our data, high resistance of chlorophyll fluorescence parameters to water loss (*i.e.* to 40% RWC and lower) suggests *S. uncinata* is highly desiccation resistant. Similarly, all parameters related to electron transport efficiency and thermal dissipation showed substantial change at the RWC of 40% and lower (*see* Figs. 6, 7). Since performance index (PI_{ABS}) is a general vitality indicator of energy transfer performance in chloroplast, it might be concluded that sufficient photosynthetic activity is maintained in *S. uncinata* at the RWC ranging 20–40% which ranks the species among desiccation resistant.

The desiccation-induced raise of ABS/RC could be interpreted as a consequence of damage/destruction of some less well functioning chlorophyll molecules in the RCs, leaving only the more efficient ones. Such response was described in poikilohydric autotrophs under *e.g.* high temperature stress (Marečková and Barták 2017). Other OJIP-derived parameters related to PSII, *i.e.* TR_0/RC and ET_0/RC declined, indicating negative effect of severe dehydration (RWC below 20%) on quinon *a* (Q_a) reduction, and photosynthetic linear electron transpor limitation.

In conclusion, it might be stated that *Sanionia uncinata*, a moss species abundant in Maritime Antarctica, might be ranked as tolerant to desiccation. The tolerance is achieved through a combination of physiological and biochemical adaptations. They are crucial for survival of the species in the harsh Antarctic environment, which includes fluctuating water availability within a growing season. Since the effects of global warming have been apparent in Maritime Antarctica over last two decades, mosses are expected to desiccate more frequently within vegetation season than in past (Robinson et al. 2000). Moreover, interaction with other factors, such as *e.g.* photoinhibition, temperature-, and freezing-tolerance must be taken into account (Perera-Castro et al. 2020) when assessing stability of the species in the Antarctic vegetation oases.

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Supplementary Materials

$$PI_{ABS} = (RC/ABS) \cdot [\varphi_{Po} / (1 - \varphi_{Po})] \cdot [\psi_0 / (1 - \psi_0)]$$

$$ABS/RC = M_0 \cdot (1 / V_J) \cdot (1 / \varphi_{Po})$$

$$TR_0/RC = M_0 \cdot (1 / V_J)$$

$$ET_0/RC = M_0 \cdot (1 / V_J) \cdot \psi_0$$

$$DI_0/RC = (ABS/RC) - (TR_0/RC)$$

Table SM1. Overview of the equations used for calculation of particular chlorophyll fluorescence parameters derived from OJIPs.