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Desiccation intensity shapes PSII recovery in the liverwort *Porella platyphylla* (L.) Pfeiff.: the effects of ABA hardening and xanthophyll cycle inhibition under light and dark conditions

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The photosynthetic responses of the poikilohydric *Porella platyphylla* (L.) Pfeiff. to desiccation are fundamental for understanding the species' survival strategy. The aim of our study was to determine (i) the extent to which one-week desiccation at different relative humidities (RH) affects the post-rehydration recovery of photosystem II (PSII) function under light and dark conditions, and (ii) the timescale on which abscisic acid (ABA) contributes to the stabilization of early photoprotection. Recovery was monitored at 1, 24 and 48 hours after rehydration using chlorophyll fluorescence parameters, and the role of zeaxanthin-dependent energy dissipation was examined by applying dithiothreitol (DTT). Our results identified three distinct recovery regimes. Samples that survived moderate desiccation (32–76% RH) and natural desiccation (rapid water loss in laboratory air, ~35% RH) almost fully restored their optimal quantum efficiency (F_v/F_m) and effective quantum efficiency (ΦPSII) values within 24–48 hours under both light and dark conditions. Desiccation at 5% RH, however, caused irreversible PSII damage, with no recovery in either light or dark. DTT markedly reduced non-photochemical quenching (NPQ), confirming the central role of zeaxanthin-dependent energy-dependent quenching (qE) in photoprotection, while also demonstrating the persistence of a DTT-insensitive NPQ fraction. A key finding of our study is that ABA hardening significantly stabilized PSII function already within 1 hour, under both light and dark conditions, resulting in higher F_v/F_m and ΦPSII values compared to untreated samples. This effect was long-lasting and remained evident throughout the 24–48-hour recovery phase, aligning with the recovery regime of the moderately desiccated samples. These results provide a new, integrated perspective on the recovery mechanisms operating during the desiccation–rehydration cycles of *P. platyphylla*, highlighting the decisive role of early ABA signalling and qE-dominated NPQ in PSII recovery following moderate dehydration.

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Introduction

Bryophytes are poikilohydric organisms, meaning that their water content equilibrates with ambient relative humidity. Many species tolerate extreme or even complete desiccation and are capable of restoring photosynthetic activity within a few hours after rehydration; this phenomenon is referred to as vegetative desiccation tolerance (VDT) (Proctor and Smirnoff 2000, Oliver et al. 2020, Xiao et al. 2026). Plants exhibiting VDT can survive prolonged periods of drying by suspending physiological processes and subsequently reactivating their metabolism upon rehydration. This capacity is largely attributable to the protective and repair mechanisms that stabilize the photosynthetic apparatus during water loss and rewetting. Since bryophytes lack the specialized tissues that provide protection against abiotic stress in tracheophytes, they predominantly rely on cell-level photoprotective processes to mitigate oxidative stress arising during desiccation–rehydration (DR) cycles (Proctor 2000a, Proctor and Smirnoff 2000, Heber et al. 2006). Mapping the physiological processes operating in such model species is of strategic importance for advancing our understanding of abiotic stress tolerance in tracheophytes (Dinakar and Bartels 2013, Oliver et al. 2020) and may ultimately contribute to the development of transgenic crops with extreme desiccation tolerance (Xiao et al. 2026).

In bryophytes, desiccation is associated with the inhibition of photosynthetic electron transport, which increases the risk of photooxidative damage. In homoiochlorophyllous bryophytes, including *Porella platyphylla*, the stability of photosystem II (PSII) depends on reversible energy-dissipating mechanisms capable of preventing photoinhibition and maintaining reaction centre (RC) integrity (Marschall and Proctor 1999, Bukhov et al. 2001, Heber et al. 2006). Non-photochemical quenching (NPQ) represents a major photoprotective mechanism that dissipates excess excitation energy. NPQ comprises several components, including the rapidly reversible energy-dependent quenching (qE), which is largely associated with zeaxanthin accumulation (Demming-Adams and Adams 1996, Horton and Ruban 2005). This process is catalysed by violaxanthin de-epoxidase (VDE), whose enzymatic activity can be selectively inhibited by dithiothreitol (DTT), thereby enabling the functional assessment of the zeaxanthin-dependent pathway (Winter and Königer 1989, Fernández-Marín et al. 2013). In several desiccation-tolerant photosynthetic organisms, zeaxanthin accumulation has been observed during dehydration, sometimes independently of light exposure, suggesting that water loss itself may trigger xanthophyll-cycle adjustments (Heber et al. 2006, Fernández-Marín et al. 2009, 2011, 2013, Verhoeven et al. 2021). The functional significance of this response appears to vary among species and ecological contexts.

In addition to xanthophyll cycle activity, abscisic acid (ABA) plays a decisive role in mediating desiccation responses, as it enhances antioxidant defence and the maintenance of osmotic balance (Mayaba et al. 2001, Dinakar and Bartels 2013, Gao et al. 2024). Exogenous ABA has been shown to enhance desiccation tolerance and improve recovery of photosynthetic performance after rehydration in several moss species, including *Atrichum androgynum* (Beckett et al. 2000, Mayaba et al. 2001, Marschall and Borbély 2011) and in a liverwort, *Dumortiera hirsuta* (Marschall and Beckett 2005). Moreover, molecular and physiological studies in *Physcomitrella patens* indicate that ABA-dependent signalling pathways are evolutionarily conserved and contribute to stress-responsive gene expression (Xiao et al. 2018, Rathnayake et al. 2019, Nibau et al. 2022). However, recent evidence suggests that endogenous ABA accumulation alone does not fully explain the acquisition of desiccation tolerance, and that drying rate and developmental context may also be critical determinants (Xiao et al. 2018). Transcriptomic analyses of resurrection plants (VDT vascular plants) indicate that ABA-dependent signalling coordinates the synthesis of late embryogenesis abundant (LEA) proteins, antioxidants and osmolytes during dehydration (Dinakar and Bartels 2013), thereby representing an evolutionarily conserved stress network. The rapid recovery of photosynthetic functionality in VDT bryophytes depends on the preservation of PSII integrity and chloroplast ultrastructure, which requires only minimal de novo protein synthesis (Proctor and Smirnoff 2000, Proctor 2001). Inhibition of VDE by DTT accelerates the decline in F_v/F_m under illumination, confirming the central role of zeaxanthin formation and trans-thylakoid pH gradient (ΔpH)-dependent energy dissipation (Winter and Königer 1989, Proctor and Smirnoff 2000).

Nevertheless, the interaction between desiccation intensity, ABA signalling and xanthophyll-cycle activity remains poorly understood in liverworts (Marschall and Beckett 2005). *P. platyphylla*, a shade-adapted species with drought tolerance in ecological terms, inhabits calcareous rock surfaces where gradual DR cycles are frequent (Marschall and Proctor 1999, Proctor 2001). Due to these characteristics, it represents an excellent model for studying the hydration thresholds separating reversible and irreversible photoinhibition, as well as early photoprotective mechanisms. Recent comparative studies have shown that VDT bryophytes partially restore optimal quantum efficiency (F_v/F_m) and effective quantum efficiency (ΦPSII) values after rehydration, suggesting that the photochemical and carotenoid-based protection of PSII relies on reversible adjustments (Perera-Castro and Flexas 2022, Esteban et al. 2024). Based on these findings, it can be assumed that dynamic NPQ regulation and ABA-mediated "priming" constitute transient strategic elements between constitutive VDT and inducible drought responses (Dinakar and Bartels 2013, Oliver et al. 2020).

Despite current knowledge, it remains unknown how desiccation thresholds, zeaxanthin-dependent qE and ABA signalling interact during the post-rehydration recovery of PSII in *P. platyphylla*. Based on this, the aims of our study were to: (i) determine the extent to which one-week desiccation of different intensities affects the post-rehydration recovery of PSII in *P. platyphylla* under light and dark conditions, with the application of VDE inhibition (DTT); and (ii) investigate the timescale and magnitude by which an exogenous ABA hardening contributes to the early stabilization of photoprotective processes in *P. platyphylla*.

Materials and Methods

Plant material

Porella platyphylla (L.) Pfeiff. (Jungermanniopsida) is a leafy liverwort exhibiting pronounced VDT (Marschall et al. 1998, Marschall és Proctor 1999), was collected from shaded, north-facing limestone rock surfaces in the Bükk Mountains (near Felsőtárkány: 47° 58' 54.6" N, 20° 26' 54.3" E). In this region, the species occurs primarily on calcareous substrates, although it can occasionally be found on tree bark as well. In its natural habitat, *P. platyphylla* experiences frequent DR cycles and is capable of restoring photosynthetic activity within 24 hours even after prolonged dry periods (Marschall and Sütő 2022).

Following taxonomic identification of the collected samples, the plants were stored at full turgor in a hydrated state in plastic containers at ~5 °C under dark (refrigerator) conditions until the start of the experiment (maximum 3–4 days). For the experiments, only thalli originating from rock surfaces were used.

Deacclimation

Since the prior environmental acclimation history of the field material was unknown, a deacclimation (dehardening) period was applied (Marschall and Sütő 2022, Stark et al. 2022). To minimize potential residual hardening effects from prior environmental exposure, the samples were maintained under fully hydrated conditions for three days (20 °C, 100% RH, 50–100 μmol m^{-2} s^{-1} photosynthetic photon flux density PPFD under the ambient natural light regime entering through the laboratory window (12/12 h photoperiod). No additional artificial illumination or direct irradiation was applied. All experiments were conducted in an air-conditioned laboratory at 20 °C. For erasing the "history" of field collected plants, at least a 24-hour deacclimation period is recommended (Austin protocol) (Stark et al. 2022). Based on our previous studies conducted

with *Porella platyphylla* (Marschall et al. 1998, Marschall and Proctor 1999, Marschall and Sütő 2022), we applied a three-day deacclimatization period at full turgor before the desiccation treatments, which proved to be sufficient (Fig. 1). During the dehardening phase, water content relative to dry mass was 1769.96 ± 220.47% (mean ± SD of the 24, 48 and 72 h values, Table 1), which, due to the presence of substantial external capillary water, greatly exceeds the water content at full turgor (273 ± 5%) reported for this species (Proctor 2000b, Marschall and Sütő 2022).

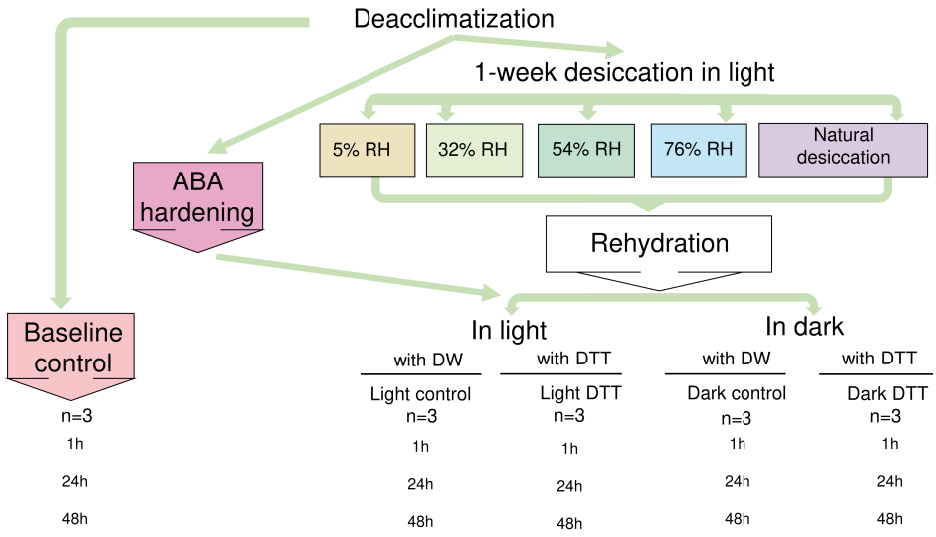

Fig. 1. Schematic overview of the experimental design used in this study.
1. ábra. A kísérlet felépítésének sematikus áttekintése.

Baseline control

After the deacclimation period, fully turgid *P. platyphylla* samples were maintained continuously under 100% relative humidity (RH) in a glass desiccator to prevent any water loss (20 °C, 50–100 μmol m^{-2} s^{-1} PPFD, see above, 12/12 h photoperiod). These samples, without undergoing drying, served as the baseline control as a function of time, representing a fully hydrated reference state following standardized deacclimation treatment. For consistency with the other treatments,

baseline control samples received the same standardized volume of distilled water (DW) applied to the thallus surface before measurements, and were exposed to identical light conditions as applied during the respective rehydration treatments.

Desiccation treatments

Samples were placed in sealed glass desiccators at the beginning of the light phase (morning) and maintained under natural diffuse daylight (50–100 μmol m^{-2} s^{-1} PPFD), following the ambient photoperiod (approximately 12 h light/12 h dark) for seven days. No additional artificial illumination or direct irradiation was applied. In controlled desiccation treatments, liverwort samples were placed under different RH conditions inside sealed glass desiccators above saturated salt solutions as follows: 76% RH – NaCl ($\Psi \approx -37.2$ MPa), 54% RH – $Ca(NO_3)_2 \cdot H_2O$ ($\Psi \approx -82.5$ MPa), 32% RH – $CaCl_2 \cdot H_2O$ ($\Psi \approx -153$ MPa), 5% RH – 54% (w/w) H_2SO_4 ($\Psi \approx -412$ MPa). Samples were placed in plastic weighing boats positioned on built-in supports within the desiccators, ensuring free air circulation inside the desiccators and preventing any physical contact with the salt medium. The laboratory maintained constant ambient temperature (20 °C), and no localized warming inside the sealed desiccators was detected during the experiment. The desiccators were kept constantly at 20 °C, away from direct sunlight and without direct exposure to heat sources.

The non-controlled desiccation treatment aimed at mimicking "natural desiccation" representing fast water loss under laboratory air (~35% RH, 20 °C, 50–100 μmol m^{-2} s^{-1} PPFD, see above, 12/12 h photoperiod, natural light infiltrating through the window) outside the desiccators. Among the five one-week desiccation treatments, all but one (76% RH) reached the cellular water-content level at which *Porella* suspends its metabolic activity, although at different drying rates. Rapid, high-intensity desiccation occurred at 5% RH and during natural desiccation (Table 1). Before the start of the experiments, the fresh weight of the liverwort samples was measured with analytical precision (0.04 g) while maintaining their full turgor (carefully blotting off excess external capillary water with tissue paper) and standardizing the external capillary water content. For each sample, fresh weight and dry weight were determined from parallel samples (n = 10) oven-dried at 105 °C for 3 h until constant weight was reached. The relative water content (RWC) of the plants was determined as follows: RWC = (actual fresh weight – dry weight) / (fresh weight at full turgor – dry weight). Samples with known fresh weight at full turgor were dried in glass desiccators containing salts in equilibrium with their saturated solutions, resulting in different relative humidities (RH) (controlled drying), and in laboratory air (natural drying) for one week (see water content as % of dry weight during the one-week dry-down in Table 1) (Marschall és Sütő 2022).

Table 1. Water content (WC) as % of dry weight in *Porella platyphylla* during the 3-day dehardening at full turgor, the 7-day drying, and 1, 24 and 48 h after rehydration. Figures are in general mean ± s.d. from three replicates. Water content of *P. platyphylla* at full turgor (% d.w.): 273 ± 5 (Proctor 2000b). Water content data were obtained under identical experimental conditions as described in Marschall and Sütő (2022).
1. táblázat. A *Porella platyphylla* víztartalma (WC) a száraz tömeg százalékában kifejezve a 3 napos stresszmentes alapállapotba visszaállás (dehardening) során teljes turgorállapotban, a 7 napos kiszárítás alatt, valamint az újranedvesítést követően 1, 24 és 48 óra elteltével. Az értékek általában három ismétlés átlagát ± szórását mutatják. A *P. platyphylla* víztartalma teljes turgorállapotban (% száraz tömeg): 273 ± 5 (Proctor 2000b). A víztartalomra vonatkozó adatokat a Marschall és Sütő (2022) munkájában leírtakkal azonos kísérleti feltételek mellett határoztuk meg.

			Water content (WC) as % of dry weight in *Porella platyphylla*		
Duration of dehardening					
24 h			1862.72 ± 222.14		
48 h			1787.34 ± 228.30		
72 h			1659.81 ± 247.78		
Time after drying	**76% RH**	**54% RH**	**32% RH**	**5% RH**	**Natural desiccation**
0 h			1659.81 ± 247.78		
6 h	1746.20 ± 1412.66	334.60 ± 205.38	38.79 ± 44.16	1.50 ± 2.59	3.53 ± 5.16
24 h	348.60 ± 551.19	11.47 ± 3.19	5.79 ± 4.43	1.12 ± 1.95	5.10 ± 3.39
31 h	32.21 ± 16.00	14.67 ± 6.94	5.94 ± 0.96	0.75 ± 1.30	5.51 ± 1.81
48 h	22.70 ± 2.24	11.47 ± 3.19	3.49 ± 0.72	0.00 ± 1.30	4.72 ± 3.12
57 h	21.85 ± 5.02	10.99 ± 3.24	1.91 ± 3.77	0.37 ± 0.65	6.10 ± 2.69
3 days	20.88 ± 3.49	11.40 ± 3.24	4.35 ± 0.46	0.00 ± 0.00	5.50 ± 3.47
5 days	23.44 ± 2.67	11.72 ± 4.56	3.09 ± 0.91	0.00 ± 0.00	5.50 ± 2.70
6 days	22.65 ± 1.21	13.87 ± 4.89	2.23 ± 1.64	0.00 ± 0.00	8.24 ± 5.10
7 days	22.62 ± 1.10	11.72 ± 4.53	2.20 ± 1.49	0.00 ± 0.00	4.72 ± 2.02
Time after rehydration			**Rehydration**		
1 h			1970.53 ± 204.33		
24 h			1864.43 ± 228.14		
48 h			1863.27 ± 222.05		

Rehydration treatments

Following one week of desiccation, the samples were rewetted by surface application of either distilled water (control) or 3 mM DTT as a VDE inhibitor. The solutions were applied dropwise in a small, standardized volume sufficient to uniformly wet each thallus using a pipette (Winter and Köniğer 1989, Proctor and Smirnoff 2000). Rehydration and recovery were carried out either under natural diurnal illumination (50–100 μmol m^{-2}, s^{-1} PPFD, 12 h light/12 h dark photoperiod) or in complete darkness at 20 °C. During light rehydration, samples recovered under natural diurnal light cycles (see above), whereas dark rehydration was conducted under complete darkness to assess PSII recovery in the absence of photon-driven processes. Measurements were taken 1, 24 and 48 hours after rehydration. Between measurements, the samples were stored in a desiccator maintaining 100% RH, thereby preventing redesiccation.

ABA treatment

Plants were pre-treated (hardened) with 0.1 mM ABA (pH 7.2) for 1 h. The ABA hardening was applied to plants at full turgor, immediately following the deacclimation protocol to ensure uniform physiological hydration status across all samples. ABA solution was applied dropwise onto the thallus surface using the same standardized protocol as for distilled water, in a small, consistent volume (1 ml) sufficient to uniformly wet each thallus without submerging the tissue. After one hour, the ABA solution was removed from the surface of the plants by rinsing with distilled water and blotting off the external capillary water with filter paper while maintaining full turgor. The ABA-treated samples (without applying a desiccation period), after removal of the ABA solution, were treated with distilled water or DTT in light or in darkness, and the photosynthetic parameters were measured after 1, 24, and 48 hours, corresponding to the rehydration times of the other desiccation-treated samples (Fig. 1). ABA hardening was conducted as a separate treatment parallel to the other desiccation treatments using fully hydrated, deacclimated samples, and it was not followed by a subsequent desiccation cycle. The purpose of this treatment was to assess the direct effect of exogenous ABA on photosynthetic parameters under fully turgid conditions, using ABA as a desiccation stress signal. Exogenous ABA was applied to fully hydrated thalli to characterize its short-term regulatory effects on photosynthetic parameters under controlled hydration, to compare the ABA-induced responses with those observed during controlled desiccation treatments, which presumably involve endogenous ABA signalling.

Chlorophyll fluorescence measurements

Chlorophyll fluorescence induction and quenching processes were examined using a DUAL-PAM-100 system (Heinz Walz GmbH, Effeltrich, Germany). Before measurements, the thalli were dark-adapted for 10 minutes at 20 °C. Initial fluorescence (F_0) was excited with weak, modulated light (0.02 μmol m^{-2} s^{-1}, 460 nm) and detected with a PIN photodiode. Maximum fluorescence (F_m) (the reduction of the all oxidized QA in PSII) was induced by a saturating light pulse of 15,000 μmol m^{-2} s^{-1} lasting 0.8 s. After the maximum fluorescence (F_m) decreased to the F_0 level, the excitation of photosynthesis was started with a white active light of 435 μmol m^{-2} s^{-1} PPFD (at 635 nm), and a quenching analysis was performed in every 50 sec. using a saturation light pulse until the steady state fluorescence level was reached.

The following parameters were calculated (Marschall and Sütő 2022):

- Optimal quantum efficiency: $F_v / F_m = (F_m - F_0) / F_m$
- Effective quantum efficiency: $\Phi PSII = (F_m' - F_s) / F_m'$
- Non-photochemical quenching: $NPQ = (F_m / F_m') - 1$
- Relative electron transport rate: $ETR(II) = \Phi PSII \times PAR \times 0.5 \times 0.84$

Statistical analysis

Measurements were carried out based on three biological replicates (n = 3). Results are presented as mean ± standard error (SE). Prior to statistical evaluation, normality was assessed using the Shapiro–Wilk test, confirming normal distribution of the dataset. Differences among desiccation treatments were evaluated using one-way analysis of variance (one-way ANOVA). The effects of DTT and light conditions during rehydration were analysed separately within each desiccation treatment using one-way ANOVA. ABA treatment, conducted as an independent experiment on fully hydrated samples, was evaluated separately using one-way ANOVA. In all cases, ANOVA was followed by the Holm–Šidák post hoc test. Statistical analyses were performed using R 4.5.2. (R Core Team 2025) software. Deviations were interpreted as significant when $p < 0.05$.

Results

Reference state: baseline control

Fully turgid, non-stressed *P. platyphylla* samples served as the baseline control, displaying consistently high PSII optimal quantum efficiency (F_v/F_m), which remained within the 0.70 ± 0.03 range at 1 h, 24 h, and 48 h (Figs 2, 3, 4, 5, 6A).

The ΦPSII likewise remained stable, falling within 0.33 ± 0.05 (Figs 2, 3, 4, 5, 6B). Non-photochemical quenching (NPQ = (F_m/F_m') – 1) stayed within 1.22 ± 0.20 (Figs 2, 3, 4, 5, 6C) throughout the observation period. To assess potential time-dependent drift in baseline control samples, linear regressions were fitted for each biological replicate (parameter vs. recovery time), and mean slopes (β ± SE) were tested against zero. F_v/F_m and ΦPSII showed negative trends that did not significantly differ from zero (F_v/F_m: β = −0.046 ± 0.020 day^{-1}, p = 0.057; ΦPSII: β = −0.088 ± 0.043 day^{-1}, p = 0.072), whereas NPQ exhibited a significant positive slope over time (β = 0.342 ± 0.078 day^{-1}, p = 0.017).

Recovery in light after rehydration with water

During the first hour of recovery in light following one week of desiccation, the optimal quantum efficiency (F_v/F_m) showed a clear gradient: the lowest values were observed in the 5% RH treatment, intermediate values occurred under the rest of the desiccation treatments (32%, 54%, 76% RH and natural desiccation), while the highest values were recorded in ABA-treated samples. The differences were significant (Fig. 2A). In the 5% RH treatment, F_v/F_m, ΦPSII, and NPQ values remained significantly lower than in all other treatments, even after 48 hours. In the 5% RH treatment, F_v/F_m and ΦPSII remained significantly lower than in all other treatments during rehydration, while NPQ values after 24–48 hours were also lower, except in the 32% RH treatment. Except for the 5% RH condition, all treatments recovered to the 0.6–0.7 F_v/F_m range during the recovery period. When examining the effective quantum efficiency (ΦPSII), three distinct value ranges were observed during the first hour of recovery, and these differed significantly from each other ($p < 0.05$). However, samples treated with ABA and those subjected to natural desiccation represented an exception, as no significant difference was detected between them. Natural desiccation samples did not differ significantly from the moderate desiccation treatments, whereas ABA-treated samples showed elevated ΦPSII values during the first hour of recovery. By the 48th hour, the significant differences disappeared among the ABA, 54% RH, 76% RH, and natural desiccation treatments during water rehydration and recovery in light (Fig. 2B). For NPQ, no significant differences were observed among the treatments (moderate desiccation and ABA) during the first hour of recovery, and this pattern persisted at 24 and 48 hours. An exception was observed in samples desiccated at 5% RH, where NPQ values declined from 24 hours onward and approached zero by 48 hours (Fig. 2C).

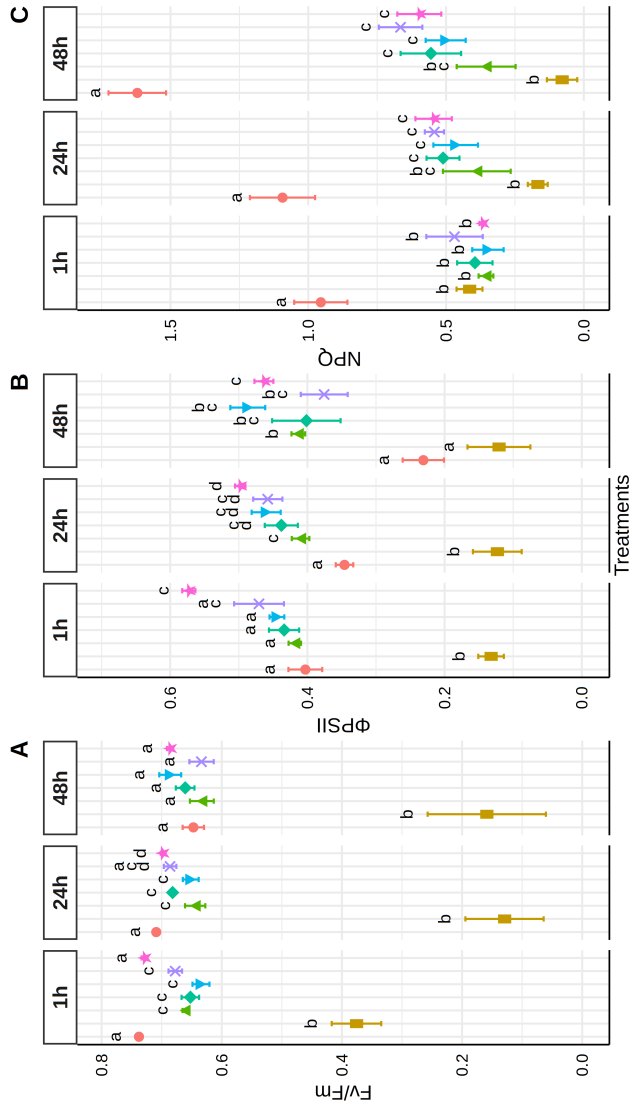

Fig. 2. Recovery in light following different levels of desiccation, measured at 1, 24, and 48 hours after rehydration with water. The baseline control indicates values measured in stress-free plants in a fully turgid state. Changes in F_v/F_m (A), ΦPSII (B), and NPQ (C) values. At a given time, values sharing the same lowercase letter are not significantly different (based on post hoc test with Holm–Šidák p-value correction, $p < 0.05$). Mean values, error bars represent ± 1 standard error ($n = 3$).

2. ábra. Fényen történő helyreállás alakulása a különböző mértékű kiszáradást követően, vízzel történő újranedvesítés során 1, 24, 48 óra elteltével: az F_v/F_m (A), a ΦPSII (B) és az NPQ (C) értékek változása. Az alapvonal kontroll a teljes turgorállapotban lévő, stresszmentes növényekben mért értékeket jelzi. Adott időpontban az azonos kisbetűt viselő kezelések értéke között nincs szignifikáns különbség (Holm–Šidák p-érték-korrekcióval végzett post hoc teszt alapján, $p < 0,05$). Átlagértékek az átlag hibaszórásával ($n = 3$).

Recovery in light with DTT application

Following one week of desiccation at 5% RH, rehydration in light under DTT treatment showed a trend similar to that observed during recovery after water rehydration in terms of F_v/F_m values: plant samples exhibited significantly lower values compared to the other treatments at 1 h, 24 h, and 48 h. In the first hour of recovery, significant differences were detected between ABA and 32%, 54% and 76% RH treatments, and between 54% RH and 76% RH. These differences disappeared by 48 hours, and, similarly to the treatments without DTT, the samples (except 32% RH) recovered to the 0.6–0.7 F_v/F_m range (Fig. 3A). The ΦPSII values in the 5% RH samples under DTT treatment also followed a pattern similar to that observed during recovery in light after water rehydration. During the first hour, ΦPSII values of the moderate desiccation samples were similar and clustered together (Fig. 3B). Under DTT treatment and light recovery, NPQ values formed distinct value ranges during the first hour after rehydration (Fig. 3C). The 32% RH samples exhibited NPQ values that converged to 0 and remained unchanged after 24 and 48 h. During recovery following desiccation at 54% and 76% RH in the presence of DTT, the NPQ values remained similar throughout the entire recovery period. During the first hour of recovery, no significant differences in NPQ values were detected among the 5% RH, ABA-treated, and natural desiccation samples; however, the moderate desiccation treatments differed significantly from ABA-treated samples. A turning point became evident at 24 h after rehydration, when the degree of desiccation differentiated the quality of recovery: at 5% RH, NPQ values approached zero by 48 h even under DTT treatment. In contrast, samples subjected to moderate desiccation reached an NPQ value range of ~0.2 at 48 h after rehydration.

Recovery in dark after rehydration with water

During recovery in darkness, similarly to the pattern observed under recovery in light, the treatments formed three value ranges during the first hour after rehydration (Fig. 4A). In the moderate desiccation treatments, F_v/F_m values did not differ significantly during the first hour of recovery under water rehydration, similarly to what was observed under light conditions. The recovery of the 5% RH samples in darkness followed the same pattern as under light at 1 h, 24 h, and 48 h after rehydration, with values remaining significantly lower than in the other treatments. During the first hour after rehydration, ABA-treated samples exhibited significantly higher F_v/F_m values than the 5% RH and moderate desiccation samples (except for 32% RH). By 48 hours after rehydration, all treatments except 5% RH showed comparable F_v/F_m values and formed a statistically

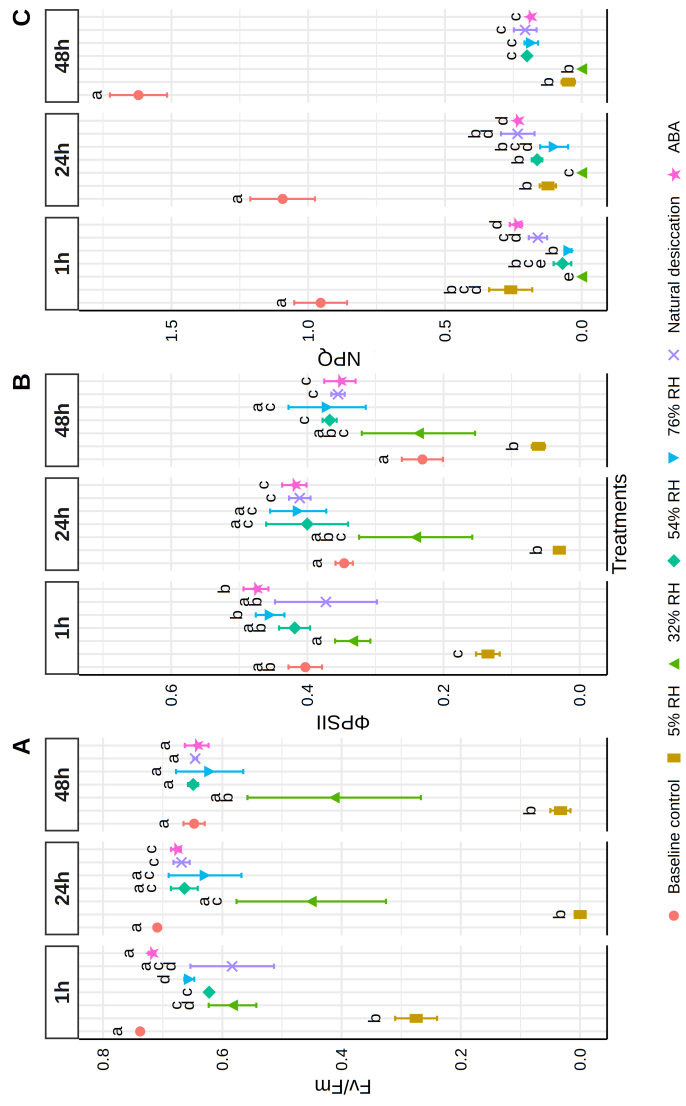

Fig. 3. Recovery in light following different levels of desiccation, measured at 1, 24, and 48 hours after rehydration with DTT. The baseline control indicates values measured in stress-free plants in a fully turgid state. Changes in F_v/F_m (A), ΦPSII (B), and NPQ (C) values. At a given time, values sharing the same lowercase letter are not significantly different (based on post hoc test with Holm–Šidák p-value correction, $p < 0.05$). Mean values, error bars represent ± 1 standard error (n = 3).

3. ábra. Fényen történő helyreállás alakulása a különböző mértékű kiszáradást követően, DTT-vel történő újranedvesítés során 1, 24, 48 óra elteltével: az F_v/F_m (A), a ΦPSII (B) és az NPQ (C) értékek változása. Az alapvonal kontroll a teljes turgorállapotban lévő, stresszmentes növényekben mért értékeket jelzi. Az F_v/F_m (A), a ΦPSII (B) és az NPQ (C) értékek változása. Adott időpontban az azonos kisbetűt viselő kezelések értéke között nincs szignifikáns különbség (Holm–Šidák p-érték-korrekcióval végzett post hoc teszt alapján, $p < 0,05$). Átlagértékek az átlag hibaszórásával (n = 3).

nearly homogeneous group, despite minor differences in mean values (including slightly lower averages at 32% RH). Similarly to recovery in light, by 48 hours the moderate desiccation samples clustered together in darkness, with no significant differences among them. Under ABA treatment, a significant difference remained between ABA and natural desiccation at 48 hours.

No significant differences in ΦPSII were detected between ABA and the moderate desiccation treatments (except for natural desiccation and 32% RH), and values ranged between 0.4 and 0.5. After 48 hours of dark recovery, ΦPSII values followed a graded response, with the lowest values at 5% RH, intermediate values under natural desiccation and 32% RH, and the highest values in the ABA, 54% RH and 76% RH treatments (Fig. 4B). During recovery in darkness with water rehydration, NPQ values showed significant differences in the first hour under ABA treatment compared to the other controlled desiccation treatments (except 32% RH) (Fig. 4C). By the 24th hour of recovery, the significant difference between ABA and 76% RH was no longer detectable, reflecting a convergence driven by decreasing NPQ values in ABA and increasing values in the 76% RH treatment. Samples desiccated at 32% and 54% RH showed stabilization of NPQ values by 24 hours after rehydration and recovered to the 0.5–0.75 range by 48 hours, reaching values comparable to those of ABA-treated plants despite distinct temporal patterns. An exception was observed in the 5% RH treatment, where NPQ values declined significantly during the 48-hour recovery period compared to the other treatments. During recovery following rehydration, NPQ values of the natural desiccation samples occupied an intermediate range together with the 5%, 32%, and 54% RH treatments. Significant differences involving the natural desiccation treatment appeared at 24 hours compared to ABA, 76% RH, and 54% RH treatments; by 48 hours, this difference persisted relative to ABA and 76% RH.

Recovery in dark with DTT application

The changes in optimal quantum efficiency following desiccation at 5% RH during recovery in darkness did not differ from the pattern observed during recovery in light under DTT treatment; the values remained significantly ($p < 0.05$) lower at 1 h, 24 h, and 48 h compared with the other treatments. The F_v/F_m recovery of ABA- and 76% RH-treated samples followed a similar pattern after rehydration, and no significant difference was detected between them throughout the monitoring period. Samples desiccated at 32%, 54% RH, as well as those subjected to natural desiccation, exhibited identical recovery at 1 h, 24 h, and 48 h, with no significant differences between them, except for a significant divergence between the 32% RH and natural desiccation treatments that emerged by 48 h. These treatments (32%, 54% RH) differed significantly from the 76% RH

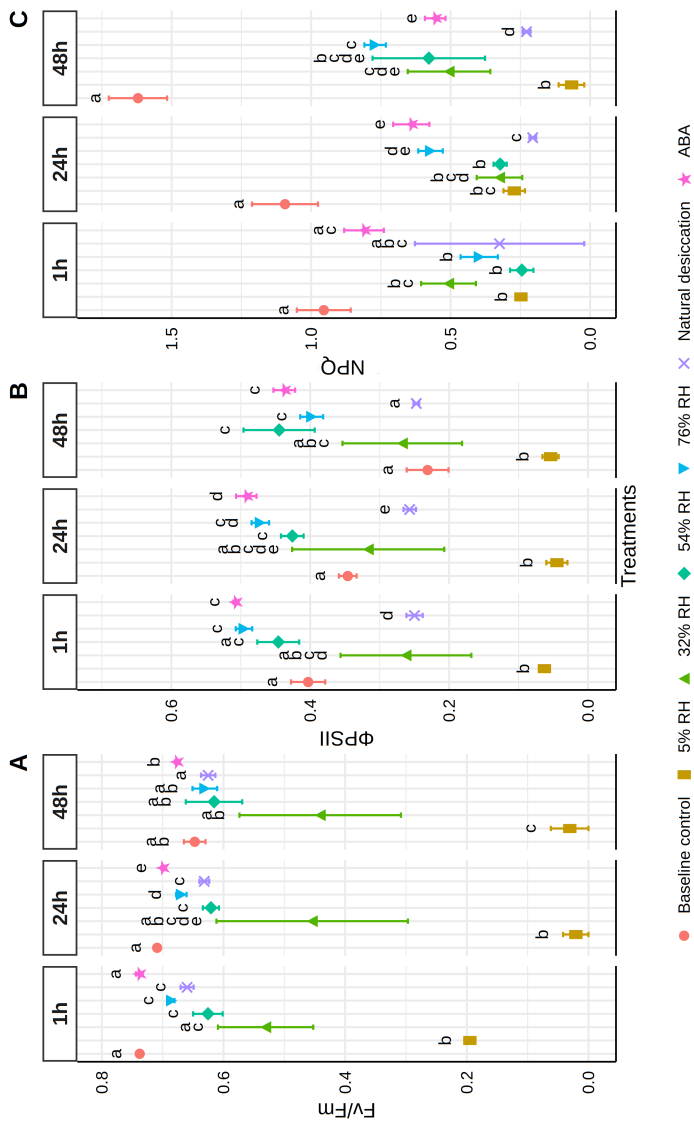

Fig. 4. Recovery in dark following different levels of desiccation, measured at 1, 24, and 48 hours after water rehydration. The baseline control indicates values measured in stress-free plants in a fully turgid state. Changes in F_v/F_m (A), ΦPSII (B), and NPQ values. At a given time, values sharing the same lowercase letter are not significantly different (based on post hoc test with Holm–Šidák p-value correction, $p < 0.05$). Mean values, error bars represent ± 1 standard error (n = 3).

4. ábra. Sötétben történő helyreállás alakulása a különböző mértékű kiszáradást követően, vízzel történő újranedvesítés során 1, 24, 48 óra elteltével: az F_v/F_m (A), a ΦPSII (B) és az NPQ (C) értékek változása. Az alapvonal kontroll a teljes turgorállapotban lévő, stresszmentes növényekben mért értékeket jelzi. Az F_v/F_m (A), a ΦPSII (B) és az NPQ értékek változása. Adott időpontban az azonos kisbetűt viselő kezelések értéke között nincs szignifikáns különbség (Holm–Šidák p-érték-korrekcióval végzett post hoc teszt alapján, $p < 0,05$). Átlagértékek az átlag hibaszórásával (n = 3).

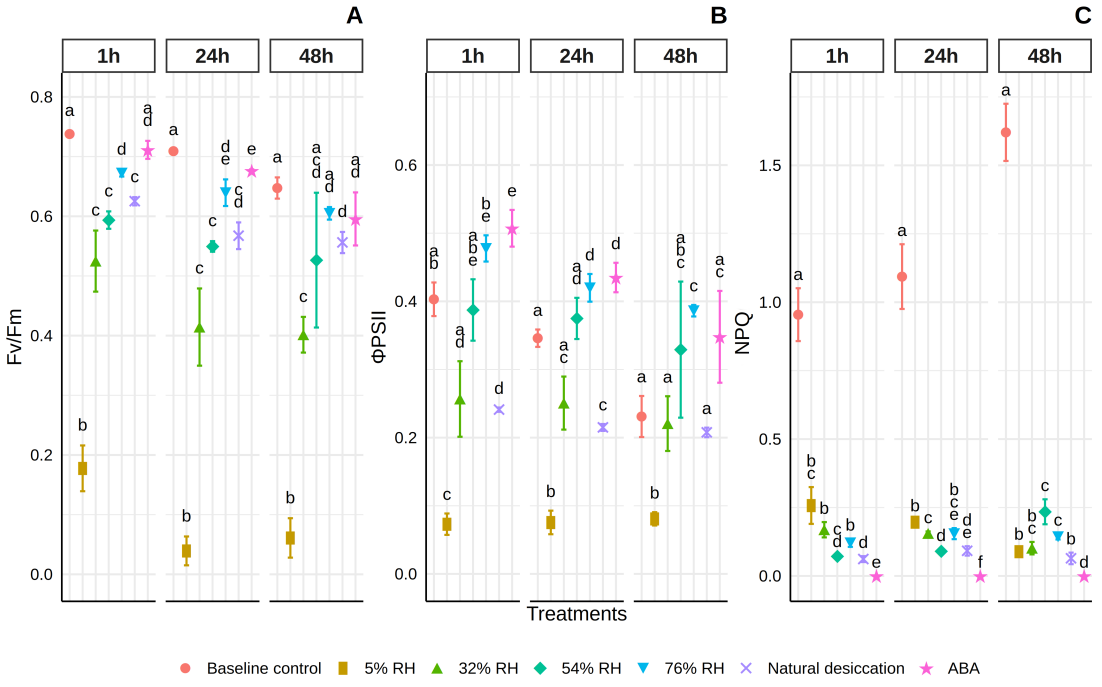

Fig. 5. Recovery in dark following different levels of desiccation, measured at 1, 24, and 48 hours after rehydration with DTT. The baseline control indicates values measured in stress-free plants in a fully turgid state. Changes in F_v/F_m (A), ΦPSII (B), and NPQ values. At a given time, values sharing the same lowercase letter are not significantly different (based on post hoc test with Holm–Šidák p-value correction, $p < 0.05$). Mean values, error bars represent ± 1 standard error (n = 3).

5. ábra. Sötétben történő helyreállás alakulása a különböző mértékű kiszáradást követően, DTT-vel történő újranedvesítés során 1, 24, 48 óra elteltével: az F_v/F_m (A), a ΦPSII (B) és az NPQ (C) értékek változása. Az alapvonal kontroll a teljes turgorállapotban lévő, stresszmentes növényekben mért értékeket jelzi. Az F_v/F_m (A), a ΦPSII (B) és az NPQ értékek változása. Adott időpontban az azonos kisbetűt viselő kezelések értéke között nincs szignifikáns különbség (Holm–Šidák p-érték-korrekcióval végzett post hoc teszt alapján, $p < 0,05$). Átlagértékek az átlag hibaszórásával (n = 3).

and ABA treatment at 24 h of recovery, and this difference remained only for the 32% RH treatment by 48 h (Fig. 5A).

Recovery in darkness under DTT treatment, in terms of ΦPSII, exhibited a similar trend to that observed under recovery in light (Fig. 5B). Samples desiccated at 5% RH consistently exhibited the lowest ΦPSII values throughout the recovery period, remaining significantly lower than in all other treatments. During recovery, plants subjected to natural desiccation and 32% RH tended to show lower ΦPSII values than those desiccated at 54% and 76% RH or treated with ABA, although differences were not consistently statistically significant. These differences persisted up to 48 h of recovery, although in the ABA treatment a significant difference remained only in comparison with the 5% RH treatment, while comparisons involving 76% RH showed a different pattern from that observed under recovery in light.

In ABA-treated plants, NPQ values under DTT treatment decreased to 0 during recovery in darkness and remained unchanged even after 48 h (Fig. 5C). During the first hour after rehydration in darkness, NPQ values showed a structured pattern across treatments. Samples desiccated at 5%, 32% and 76% RH exhibited similar values and clustered together, whereas samples subjected to 54% RH and natural desiccation formed a second group with comparable values. Following rehydration, NPQ values for all treatments (except ABA) remained within the 0.05–0.25 range at 24 and 48 h. No significant difference was detected between the 5% RH and natural desiccation treatments at the 48-hour recovery point; however, both differed significantly from the 54% RH and 76% RH treatments.

To facilitate comparison among dehydration and ABA treatments across light and dark conditions and DTT treatment, the values of F_v/F_m, ΦPSII, and NPQ at the 48 h recovery time point are summarized in Fig. 6. In comparison, the limitation of zeaxanthin formation caused a greater reduction in NPQ values than the effect of light or darkness during rehydration (Fig. 6C).

Discussion

The baseline control samples remained fully hydrated throughout the experimental period; a gradual change in PSII-related parameters was observed over time. Sustained hydration in desiccation-tolerant mosses has been reported to alter physiological balance and photosynthetic regulation (Proctor and Smirnoff 2000), which could explain the gradual decline in F_v/F_m and the increase in NPQ observed in the control samples during the experiment. While deacclimation kinetics may vary among bryophytes (Wood 2007, Stark et al. 2014, Stark 2017, Morales-Sánchez et al. 2022, Nava-Nolazco et al. 2025), earlier work on *P.*

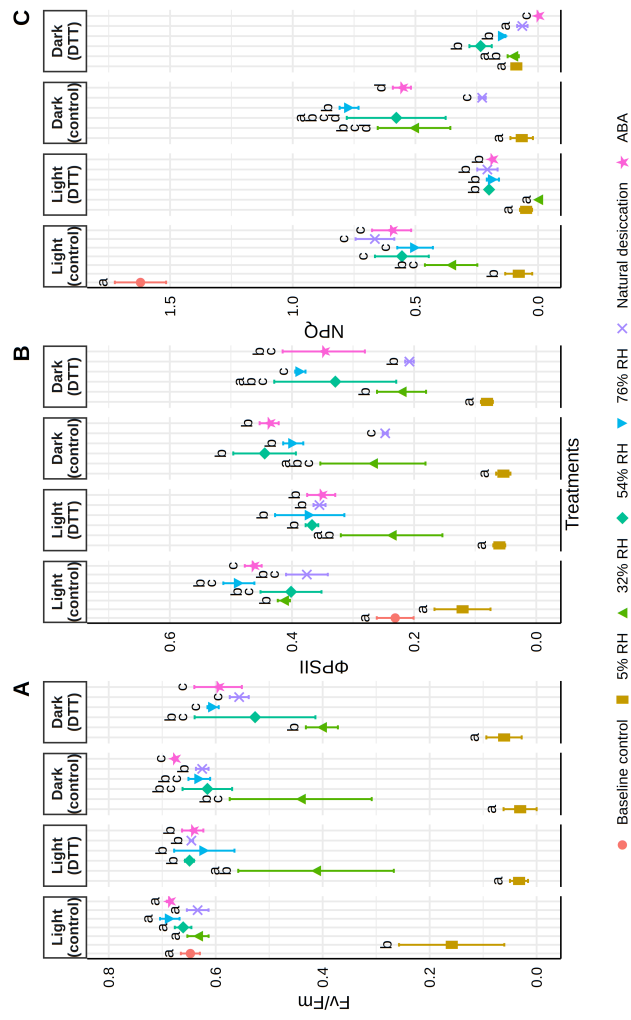

Fig. 6. Photosynthetic parameters at the 48 h recovery stage across dehydration treatments. Values of F_v/F_m (A), ΦPSII (B) and NPQ (C) are shown for the different RH treatments and ABA under light and dark conditions, with and without DTT. Different letters indicate significant differences among treatments within the same experimental group (post hoc test with Holm–Šidák p-value correction, $p < 0.05$). Statistical comparisons were performed within experimental groups only; cross-condition comparisons (water vs. DTT) are presented for visualization purposes. Mean values, error bars represent ± 1 standard error (n = 3).

6. ábra. A fotoszintetikus paraméterek alakulása az újranedvesedési helyreállás 48. órájában a különböző kiszárítási kezelések után. Az F_v/F_m (A), ΦPSII (B) és NPQ (C) értékei a különböző RH-kezelések és az ABA hatására kerülnek bemutatásra fényen és sötétben, DTT jelenlétében és hiányában. Az eltérő betűk az azonos kísérleti csoporton belüli kezelések között szignifikáns különbséget jeleznek (post hoc teszt Holm–Šidák p-érték-korrekcióval, $p < 0,05$). A statisztikai összehasonlításokat kizárólag az egyes kísérleti csoportokon belül végeztük; a különböző feltételek (kontroll vs. DTT) közötti összehasonlítások kizárólag szemléltetési céllal szerepelnek. Átlagértékek az átlag hibaszórásával (n = 3).

platyphylla demonstrated that a three-day fully hydrated period is sufficient to restore PSII functionality and baseline fluorescence parameters (Marschall and Sütő 2022). The dehardening period applied in this study provided full deacclimation of the field-collected plants before drying treatments.

The patterns described above suggest that desiccation intensity, NPQ regulation and ABA signalling interact during PSII recovery, forming an integrated physiological response during rehydration. Within this framework, three distinct recovery regimes can be distinguished, defined by the severity of desiccation and the resulting physiological state of PSII during rehydration: (i) a collapse regime characterized by irreversible PSII damage after extreme desiccation (5% RH), (ii) a reversible recovery regime observed after moderate desiccation (32–76% RH), and (iii) a gradual recovery regime associated with natural desiccation conditions. These regimes define the post-rehydration PSII restoration of *P. platyphylla*. After one week of desiccation at 5% RH, F_v/F_m remained persistently below 0.4, and ΦPSII stayed around 0.15 even 48 hours after rewetting, indicating irreversible PSII damage. Such a collapse is consistent with oxidative injury to the D1 protein and the redox components of the RC, resulting from sustained reactive oxygen species (ROS) stress during extreme desiccation (Heber et al. 2006, Oliver et al. 2020). Under extremely low water availability, PSII structural integrity cannot be maintained even in the presence of protective mechanisms, explaining irreversible photoinhibition under severe desiccation stress (Oliver et al. 2020, Jabłońska et al. 2023). The collapse observed in the 5% RH treatment was more severe than that reported for *Physcomitrium patens* (Xiao et al. 2026).

During rehydration with water under light conditions, after 24 hours all moderately desiccated samples showed values approaching the F_v/F_m and ΦPSII levels characteristic of unstressed plants. In contrast, under dark conditions, F_v/F_m remained lower in samples treated at 32% RH, in naturally desiccated samples, and in those treated at 54% RH. ΦPSII recovered in the ABA-, 76% RH-, and 54% RH-treated samples, but not in the 32% RH-treated or naturally desiccated samples. When samples were rehydrated under light in the presence of a violaxanthin cycle inhibitor, only the 32% RH-treated samples failed to recover their F_v/F_m and ΦPSII values within 24 hours; under all other (moderate desiccation) treatments, values essentially reached or closely approached those typical of unstressed plants. In the presence of a violaxanthin cycle inhibitor under dark conditions, the maximum quantum efficiency (F_v/F_m) approached unstressed levels in the ABA- and 76% RH-treated samples, but not in the other treatments. Similarly, the effective quantum efficiency (ΦPSII) reached unstressed levels in the ABA- and 76% RH-treated samples, whereas in the remaining treatments it also failed to attain values characteristic of unstressed plants. This pattern corresponds to reversible photoinhibition, where RC structure remains preserved, and damage is largely confined

to donor- and acceptor-side redox components and transient uncoupling between the antenna and the RC (Proctor and Smirnoff 2000, Morales-Sánchez et al. 2022, Perera-Castro and Flexas 2022). The recovery of *P. platyphylla* at 32–76% RH resembles that described for *Racomitrium canescens* (Peng et al. 2023), although it is weaker than the extreme VDT capacity for *Syntrichia caninervis* (Yang et al. 2023). Desiccation tolerance in mosses depends on cell wall elasticity, membrane flexibility and the restorative capacity of chloroplast ultrastructure during early rehydration (Morales-Sánchez et al. 2022, Perera-Castro and Flexas 2022). The recovery patterns of F_v/F_m and ΦPSII in light, in the natural desiccation treatment, resembled those observed at 54–76% RH, indicating that *P. platyphylla* tolerates the rapid water loss characteristic of shaded carbonate rock microhabitats (Marschall and Proctor 1999, Proctor 2000b). Although the final hydration levels of the 32% RH and natural desiccation treatments were comparable, their recovery responses slightly differed, depending on the rehydration conditions and phase, likely because samples dried under laboratory air lost water more rapidly during the first 6 hours than those dried at 32% RH. When desiccated at 76% RH, *P. platyphylla* remained fully turgid during the first 26 hours, while plants dried at 54% RH maintained full turgor during the first 6 hours, losing only their external capillary water. In contrast, plants dried at 32% RH, 5% RH, or under laboratory air lost full turgor within the first 5 hours. These latter treatments resulted in very rapid and intense dehydration. By the 6th hour of desiccation, plants treated at 32% RH had an RWC of about 40%, whereas those dried under laboratory air reached 3–4% RWC, and those exposed to 5% RH retained only 1–2% RWC. In natural habitats, desiccation proceeds gradually under fluctuating microclimatic conditions, enabling partial physiological preconditioning, whereas controlled desiccation at fixed 32% RH imposes a more abrupt dehydration regime that may limit protective responses (Proctor and Smirnoff 2000, Oliver et al. 2020). A water content of *P. platyphylla* below 15% d.w. largely represents cytoplasmic-bound water that is not available for metabolic activity. Plants in all drying treatments (except 76% RH) reached this level, although at different rates. Dehydration occurred most rapidly (within 5 h) in the 5% RH and natural desiccation treatments. Under these conditions, *P. platyphylla* required only five hours to reach an air-dried state. Such differences in desiccation kinetics may influence PSII stability and recovery. These recovery patterns provide the physiological context for understanding the role of photoprotective NPQ regulation during rehydration.

Across all treatments, DTT application substantially reduced NPQ, indicating that the predominant portion of NPQ capacity in *P. platyphylla* depends on VDE-driven violaxanthin-antheraxanthin-zeaxanthin conversion. In the canonical xanthophyll-cycle model, thylakoid lumen acidification (ΔpH) activates VDE

and promotes zeaxanthin accumulation, which together with LHCSR (Light-Harvesting Complex Stress-Related, the canonical qE effector in non-angiosperms) and/or PsbS (the pH-responsive PSII subunit that initiates qE in vascular plants and operates additively with LHCSR in bryophytes), enables rapid qE-type energy dissipation (Demmig-Adams and Adams 1996, Horton and Ruban 2005, Fernández-Marín et al. 2013). The small residual NPQ observed under DTT treatment indicates zeaxanthin-independent components, previously discovered in *P. platyphylla* under both light (Marschall and Sütő 2022) and dark recovery. Our results further suggest that the xanthophyll cycle in the leafy liverwort *P. platyphylla* may remain operative and reversible even in the complete absence of light during a desiccation–rehydration cycle. Zeaxanthin formation during desiccation in darkness therefore appears to be independent of the trans-thylakoid pH gradient and the associated conformational change of the PsbS protein. Although Verhoeven et al. (2021) did not detect dark violaxanthin de-epoxidation in three liverworts (*Marchantia polymorpha*, *Pellia epiphylla*, and *Lunularia cruciata*) or in the green alga *Ulva rigida*, our results in *P. platyphylla* indicate the presence of a DTT-insensitive NPQ component during light and dark recovery, which may reflect zeaxanthin formation. Several hypotheses have been proposed to explain dark activation of VDE, including the possible presence of multiple VDE isoforms. Studies on lichens have demonstrated that desiccation can activate photoprotective mechanisms associated with conformational rearrangements of pigment–protein complexes (Heber 2008), suggesting that a related process may also facilitate VDE activation. This mechanism may be induced during dehydration to protect chlorophyll during desiccation and to facilitate rapid acclimation upon rehydration (Fernández-Marín et al. 2009). However, zeaxanthin accumulation has also been reported in species that are not strongly desiccation-tolerant, suggesting that its presence alone does not fully explain desiccation tolerance (Verhoeven et al. 2021). Similar mechanisms occur in bryophytes: *Syntrichia ruralis* maintains partial NPQ through thermally stabilized "glassy-state" mechanisms (Winter and Königer 1989, Fernández-Marín et al. 2013, Lu et al. 2022), whereas in *Physcomitrium patens* LHCSR proteins partly compensate reduced zeaxanthin through pH-dependent conformational changes (Ndhlovu et al. 2025). In addition to carotenoid-dependent photoprotection, hormonal regulation may also contribute to PSII stabilization during early recovery.

In thalli recovering under light during rehydration, ABA-treated samples showed higher ΦPSII and more stable NPQ already in the first hour, indicating an early regulatory effect of ABA on photoprotective processes. Similar rapid responses in bryophytes (Marschall and Beckett 2005, Marschall and Borbély 2011) and resurrection vascular plants are associated with enhanced antioxidant capacity, LEA protein accumulation and improved redox stability (Mayaba et al.

2001, Dinakar and Bartels 2013, Gao et al. 2024), processes linked to the canonical ABA receptor cascade (PYR/PYL/RCAR–PP2C–SnRK2 module) in land plants (Sun et al. 2020, Takezawa et al. 2011, Zimran et al. 2025). In liverworts, B3 Raf kinases may further regulate VDT and dormancy (Jahan et al. 2022), while early antioxidant activation and LEA accumulation can reduce ROS formation around PSII (Mayaba et al. 2001, Gao et al. 2024) and stabilize membranes during initial rehydration (Beckett et al. 2000, Ćosić et al. 2020). During the 1–24 h recovery phase, such ABA-associated responses coincide with gradual stabilization of photosynthetic performance, similar to the coordinated recovery described in VDT mosses including *Racomitrium canescens* and *Syntrichia caninervis* (Nibau et al. 2022, Peng et al. 2023, Yang et al. 2023), and similarly reflected in our data by the higher ΦPSII values at 24 hours of rehydration. Upon rehydration under light conditions, after 24–48 h, the F_v/F_m and ΦPSII values of ABA-treated samples were similar to those of the other moderately desiccated samples, whereas under dark conditions, they were in the same range as those treated at 76% and 54% RH. This suggests that early ABA signalling may influence subsequent recovery dynamics of PSII (Oliver et al. 2020, Niu et al. 2025). Together, these observations suggest that PSII recovery in *P. platyphylla* emerges from the interaction of desiccation intensity, NPQ dynamics and hormonal regulation.

Interactions between desiccation intensity, NPQ regulation and ABA signalling

One of the central outcomes of this study is that desiccation intensity, NPQ dynamics and ABA-mediated responses together determine distinct recovery patterns in PSII performance. Under moderate desiccation, the structural integrity of RCII and the thylakoid membranes is largely preserved (Pressel and Duckett 2010), enabling rapid reactivation of zeaxanthin-dependent qE-type NPQ after rehydration and the establishment of a high NPQ capacity that dissipates excess excitation and maintains the PSII acceptor side in a safe redox state. ABA may further enhance this stabilization by modulating redox balance and protective processes, resulting in higher and more stable ΦPSII and F_v/F_m values during the 48-hour recovery period. In this system, carotenoid-based photoprotection and hormonal regulation function as partially redundant protective layers that support PSII stability (Oliver et al. 2020, Lu et al. 2022, Gao et al. 2024). In contrast, the extremely severe desiccation imposed by the 5% RH treatment involves rapid water loss associated with extensive membrane and protein damage that prevents restoration of PSII functionality. The resulting disruption of thylakoid organization, chloroplast membrane integrity and stromal metabolism leads to irreversible photochemical failure (Heber et al. 2006, Oliver et al. 2020, Bartels et al. 2025, Zuo 2025).

Positioning *Porella platyphylla* in the bryophyte VDT spectrum

Our results suggest that *P. platyphylla*, which occurs in shaded, mesophilic microhabitats in its natural environment (Marschall and Proctor 1999, Proctor 2001), does not reach the extreme desiccation tolerance of desert mosses such as *Syntrichia caninervis* (Yang et al. 2023). Based on the comparison of rehydration recovery patterns, the desiccation treatments conducted at different relative humidity levels, the ABA responses and the qE-dominant NPQ capacity collectively indicate that the species occupies the mid-range of the extreme VDT continuum. The recovery pattern suggests a contribution of both constitutive and inducible mechanisms under moderate water loss (Oliver et al. 2020, Bartels et al. 2025). In all drying treatments (except 76% RH), plants reached water contents corresponding to cytoplasmic-bound water, although at different rates. Cytoplasmic-bound water is unavailable for metabolic activity. Because the different desiccation treatments inherently represent different drying rates, exposure to different relative humidity levels combines differences in dehydration intensity with differences in drying dynamics. The rapid recovery of zeaxanthin-dependent qE and the early stabilizing effect of ABA adequately explain the restoration of PSII functions following moderately intense desiccation treatments, whereas the species is unable to compensate for the structural damage caused by extremely intense and prolonged desiccation.

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A kiszárítás intenzitásának meghatározó szerepe a II-es fotokémiai rendszer helyreállásában fényen és sötétben: az abszcizinsav-kezelés és a xantofill-ciklus gátlásának hatása a *Porella platyphylla* (L.) Pfeiff. májmohában

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Kulcsszavak: ABA-jelátvitel, ABA-kezelés, ditiotreitol, fényvédelem, kiszáradási-újranedvesedési ciklus, PSII helyreállási dinamika.

Összefoglalás: A poikilohidrikus leveles májmoha *Porella platyphylla* (L.) Pfeiff. kiszáradásra adott fotoszintetikus válaszai kulcsfontosságúak a faj túlélési stratégiájának megértésében. Vizsgálatunk célja az volt, hogy meghatározzuk: (i) az egyhetes, eltérő relatív páratartalmon végzett kiszárítás milyen mértékben befolyásolja a PSII működésének újranedvesítés utáni helyreállását fényen és sötétben; valamint (ii) az abszcizinsav (ABA) milyen időléptékben járul hozzá a korai fényvédelem stabilizálásához. A regenerációt a rehidratációt követő 1., 24. és 48. órában klorofill-fluoreszcencia paraméterek segítségével követtük nyomon, és a zeaxantin-függő energiadisszipáció szerepét ditiotreitol (DTT) alkalmazásával vizsgáltuk. Eredményeink három eltérő helyreállási tartományt különítettek el. A mérsékelt kiszáradást túlélő minták (32–76% RH), valamint a természetes kiszáradásnak kitett minták (gyors vízvesztés laboratóriumi levegőn, ~35% RH) optimális kvantumhatásfokuk (F_v/F_m) és effektív kvantumhatásfokuk (ΦPSII) értékeit fényben és sötétben egyaránt szinte teljes mértékben helyreállították 24–48 órán belül. Ezzel szemben az 5% RH mellett történő kiszáradás irreverzibilis PSII-károsodást okozott, és sem fényben, sem sötétben nem következett be regeneráció. A DTT jelentősen csökkentette a nem-fotokémiai kioltást

(NPQ), megerősítve a zeaxantin-függő, energiadependens kioltás (qE) központi szerepét a fényvédelemben, továbbá kimutatva egy DTT-re nem érzékeny NPQ-frakció fennmaradását is. Vizsgálatunk egyik kulcsfontosságú eredménye, hogy az ABA-kezelés már 1 órán belül jelentősen stabilizálta a PSII működését mind fényben, mind sötétben, ami a kezeletlen mintákhoz képest magasabb F_v/F_m- és ΦPSII-értékekben nyilvánult meg. Ez a hatás tartósnak bizonyult, és a 24–48 órás helyreállási szakasz során is megfigyelhető maradt, összhangban a mérsékelt kiszáradást elszenvedő minták újranedvesedési mintázatával. Eredményeink új, integrált megközelítést nyújtanak a *P. platyphylla* kiszáradási–újranedvesedési ciklusai során működő regenerációs mechanizmusok megértéséhez, kiemelve a korai ABA-jelátvitel és a qE-domináns NPQ meghatározó szerepét a PSII mérsékelt dehidratációt követő helyreállásában.

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Abbreviations

ABA: abscisic acid; ANOVA: analysis of variance; D1: PSII core D1 protein; DR: desiccation–rehydration cycle; DT: desiccation tolerance; DTT: dithiothreitol; DW: distilled water; d.w.: dry weight; ETR(II): relative electron transport rate of Photosystem II; F_m: maximum fluorescence; F_s: steady-state fluorescence; F_0: initial fluorescence; F_m': maximum fluorescence in the light-adapted state, F_0': minimum fluorescence in the light-adapted state; F_v/F_m: optimal quantum efficiency of PSII; LEA: late embryogenesis abundant (proteins); LHC: light-harvesting complex; LHCSR: light-harvesting complex stress-related proteins; MPa: megapascal; NPQ: non-photochemical quenching ($NPQ = (F_m/F_m') - 1$), PAR: photosynthetically active radiation; PPFD: photosynthetic photon flux density, PP2C: protein phosphatase 2C; PSII: photosystem II; PsbS: PSII subunit S; PYR/PYL/RCAR: ABA receptors (PYR/PYL/RCAR family); qE: energy-dependent quenching (fast NPQ component); qI: slow/photoinhibitory component of NPQ; qP: photochemical quenching coefficient; RC: reaction centre, RCII: reaction centre of Photosystem II; RH: relative humidity; ROS: reactive oxygen species, SE: standard error; SnRK2: SNF1-related protein kinase 2; VDE: violaxanthin de-epoxidase; VDT: vegetative desiccation tolerance; ΔpH: trans-thylakoid pH gradient; ΦPSII: effective quantum efficiency