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Dehydration and rehydration differently affect photosynthesis and volatile monoterpenes in bryophytes with contrasting ecological traits

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Abstract

Bryophytes desiccate rapidly when relative humidity decreases. The capacity to withstand dehydration depends on several ecological and physiological factors. Volatile organic compounds (VOCs) may have a role in enhancing tolerance to desiccating bryophytes. However, the functions of VOCs in bryophytes have received little attention so far. We aimed to investigate the impact of a dehydration-rehydration treatment on primary carbon metabolism and volatile terpenes (VTs) in three bryophytes with contrasting ecological traits: *Vessicularia dubyana*, *Porella platyphylla* and *Pleurochaete squarrosa*. First, we confirmed the desiccation sensitivity gradient of the species. Under fully hydrated conditions, the photosynthetic rate (A) was inversely associated with stress tolerance, with a lower rate in more tolerant species. The partial recovery of A in *P. platyphylla* and *P. squarrosa* after rehydration confirmed the desiccation tolerance of these two species. On the other hand, A did not recover after rehydration in *V. dubyana*. Regarding VT, each species exhibited a distinct VT profile under optimum hydration, with the highest VT pool found in the more desiccation-sensitive species (*V. dubyana*). However, the observed species-specific VT pattern could be associated with the ecological habitat of each species. *P. squarrosa*, a moss of dry habitats, may synthesize mainly non-volatile secondary metabolites as stress-defensive compounds. On the other hand, *V. dubyana*, commonly found submerged, may need to invest photosynthetically assimilated carbon to synthesize a higher amount of VTs to cope with transient water stress occurrence. Further research on the functions of VTs in bryophytes is needed to deepen our understanding of their ecological significance.

1 | INTRODUCTION

Bryophytes (hornworts, liverworts and mosses) cover wide areas of the Earth, from the poles to the tropics, thus habiting a wide range of environments, including woodlands and boreal and temperate forests. Despite their small size and simple structure (generally unistratose leaves or thalli), bryophytes are a key group in many ecological processes: controlling soil and vegetation hydrology and temperatures

(Beringer et al., 2001), preventing soil erosion (Belnap et al., 2001), entrapping CO_2, thus influencing the productivity of ecosystems (Elbert et al., 2012), providing soil nitrogen input by hosting nitrogen-fixing bacteria (Kurina & Vitousek, 2001), and contributing significantly to the quantity of above-ground biomass (Belnap et al., 2001). However, compared to tracheophytes (i.e., vascular plants), bryophytes show lower photosynthetic rates (A) (Martin & Adamson, 2001). This is mainly due to their particular foliar structure, which is based on a single layer of photosynthetic cells (except the midrib in bryophytes of the order Polytrichales). Bryophytes also show relatively high dark mitochondrial respiration rates (Rd) in comparison to A (Wagner et al., 2013; Wang & Bader, 2018).

Photosynthesis and other physiological processes are ultimately dependent on water availability in plants. In bryophytes, such a dependency is made particularly clear because of the lack of mechanisms (i.e., stomata, cuticle, efficient internal water transport) that actively control and regulate the internal water content, which fluctuates in equilibrium with the water available in the surrounding environment. As a consequence of the inability to control water loss, bryophytes are rapidly desiccated when air relative humidity decreases, and therefore, their physiological processes are inhibited by dry conditions (i.e., when tissues dehydrate; Oliver & Mishler 2000) while being activated in humid environments (i.e., by hydration). However, most bryophytes, so-called desiccation-tolerant (DT), usually tolerate water loss. These species possess the remarkable ability to completely desiccate below a relative water content (RWC) of ~30% or an absolute water content of 0.1 g H_2O g^{-1} dry weight (Farrant et al., 2017). Upon rehydration, they recover their physiological functions (Alpert, 2000) by slowly resuming metabolism (to pre-desiccation state; Cruz De Carvalho et al., 2014). Vegetative desiccation tolerance helps bryophytes cope (without resorting to spores) with recurrent dry periods and short-term drought events. Other bryophytes, mainly living in aquatic environments, are desiccation-sensitive (DS) and do not withstand such a dramatic reduction in water availability. This reflects the early origin of bryophytes, pre-dating vascular flora appearance, and the transition of plants from an aquatic environment to the land (Morris et al., 2018; Oliver et al., 2005). Indeed, the degree or even the accomplishment of the desiccation tolerance depends on several biological and environmental factors during the drying and hydration periods. Biological factors include species ecology, life phases and intraspecific differences (Coe et al., 2021; Marks et al., 2021). Environmental factors, such as microclimatic conditions, the length of the recovery period, and as well as the level of air humidity during rehydration, play a crucial role in determining tolerance to desiccation (Stark, 2017). This implies that even some DT species might only withstand drying after an acclimation phase. On the other hand, *Fontinalis antipyretica*, an aquatic bryophyte previously described as DS, can resume normal photosynthetic performance following slow drying and rehydration (Cruz de Carvalho et al., 2011; Cruz De Carvalho et al., 2012). Bryophytes of sun-exposed (and generally also dry) sites can usually withstand faster dehydration rates because they are constitutively DT, whereas bryophytes living in shady ecological habitats are more sensitive to desiccation (Cruz De Carvalho et al., 2012). Overall, desiccation is not a dual trait (DT or DS) because great plasticity exists across populations or even in individual plants (Marks et al., 2021). Matching species plasticity with environmental pressure is key to explaining the response observed in nature and reproduced experimentally.

During dehydration, the activation of the physiological mechanisms of tolerance in bryophytes causes a decrease in A and a slowdown of the whole metabolism (Mayaba et al., 2001). In order to limit the damage following desiccation (mostly oxidative and structural) and to preserve physiological integrity while drying, bryophytes activate several photoprotective strategies (Fernández-Marín et al., 2016; Oliver et al., 2000). These include a cytoplasm state change to vitrification (Dinakar & Bartels, 2013), the accumulation of non-structural carbohydrates and other compatible solutes (Oliver et al., 2005), the activation and synthesis of specific stress proteins (i.e., dehydrins; Qin Wang et al., 2009), and the generation of other protective metabolites such as phenolic compounds (Cruz de Carvalho et al., 2017) or isoprenoids (i.e., tocopherols and carotenoids) that act as antioxidants and membrane stabilizers (Beckett et al., 2012; Beckett & Minibayeva, 2008). Recently, the carotenoid zeaxanthin has been found to play a role in sustained forms of thermal dissipation in DT bryophytes (Verhoeven et al., 2020), thus contributing to the protection of their photosynthetic apparatus.

Volatile organic compounds (VOCs) are also important players in the protection against oxidative stresses and may be implicated in the response to desiccation (Beckett et al., 2012). In particular, volatile terpenes (VTs, i.e. isoprene, monoterpenes and sesquiterpenes) (Loreto & Schnitzler 2010) have been demonstrated to mediate the oxidative status at several levels (Vickers et al., 2009) mainly by (1) stabilizing membranes (Sharkey & Singsaas, 1995) through reduction of either membrane stiffness (Pollastri et al., 2019) or lipid peroxidation and downstream oxidative bursts (Velikova et al.,2012); and (2) quenching reactive oxidative species (ROS, Vickers et al., 2009), thus acting as direct antioxidants (Ledford & Niyogi, 2005; Velikova et al., 2016). VT biosynthesis and profiles have already been relatively well characterized in angiosperms (Harrison et al., 2013) and, more recently, in green algae (Dani & Loreto, 2017). However, VT production in bryophytes has received little attention so far (Barlow et al., 2005; Chen et al., 2018; Sharkey et al., 2008; Sharkey &Monson, 2017).

Although considerable progress has been made in understanding the protection during the desiccation processes (Proctor et al., 2007a and references herein), whether VTs improve desiccation resistance or the capacity to rehydrate still needs to be explored. To the best of our knowledge, no study has addressed the response of VT production to desiccation in bryophytes to date. This has only been considered in a few cases in tracheophytes, including the poikilochlorophyllous resurrection angiosperm *Xerophyta humilis* (Beckett et al., 2012), and some filmy ferns (Fam. Hymeophyllaceae) (Niinemets et al., 2018). Despite such limited research, VTs from bryophytes appear to have similar functions to those found in tracheophytes (Chen et al., 2018).

This work aimed to investigate the impact of a dehydration-rehydration treatment in bryophytes with different desiccation sensitivities and from a range of habitats on (1) photosynthetic performance by continuously monitoring CO_2 assimilation during desiccation, and (2) VT changes in both relative and absolute amounts, after exposure to dehydration and rehydration. We hypothesized that (1) bryophytes more

tolerant to desiccation show better photosynthetic performance under water deprivation and that (2) VT fingerprint may be species-specific and linked to the environmental pressures of their natural habitat. To fulfil our goals, we selected bryophyte species with differential and contrasting habitats and attributes (Hill et al., 2007) (1) the moss *Pleurochaete squarrosa* (Brid.) Lindb., a species living in light-exposed environments and often found in dry places; (2) the liverwort *Porella platyphylla* (L.) Pfeiff., a semi-shade plant, rarely living in full light and generally preferring well-drained terrestrial substrate; and (3) the moss *Vessicularia dubyana* Broth., usually found in slow-moving water currents in rivers with areas of intense shade, as well as in the depths of lagoons, lakes and small streams, as it is a submerged species that occasionally emerges and can survive intermittent desiccation events.

2 | MATERIALS AND METHODS

2.1 | Plant material and acclimation to laboratory conditions

Intact mono-specific canopies of the moss *P. squarrosa* (Pottiaceae; acrocarpic) and the liverwort *P. platyphylla* (Porellaceae; foliose) were collected from a site with minimal human impact (Tertanga, Bizkaia, Spain; 42°58´ N, 3°01´ W, elevation 500 m). The material was stored in polyethylene containers under a high-humidity atmosphere and transported to the laboratory in a portable icebox (temperature below 5°C). Once in the laboratory, all the collected bryophytes were cleaned of debris and sediments with distilled water and fully rehydrated (sprayed with distilled water) and maintained for 5 days under controlled conditions to allow acclimation to laboratory conditions (high relative humidity = 90–100%, moderate irradiance = 100 µmol photons m^{-2} s^{-1} with a photoperiod of 12:12 h, and temperature = 18–20°C) (Stark, 2017). The moss *V. dubyana* (Hypnaceae; phyllids) was purchased from a local aquarium shop (Sesto Fiorentino, Italy) and transported to the laboratory in a portable icebox. As this species is aquatic, it was kept in water during the acclimation period under the same controlled environmental conditions as described above. This acclimation period was necessary for performing dehydration experiments (Stark, 2017).

2.2 | Experimental design: desiccation and rehydration simulation

We set up an experiment to standardize and simulate the desiccation and rehydration processes that may occur under natural conditions. We followed the recommendations for best practices in bryophyte studies of photosynthesis (Rice & Cornelissen, 2014). Bryophyte canopies of 5 cm^2 surface area (each considered as a replicate, n = 3–7, unless otherwise stated) were placed in an air-tight round-shaped glass gas exchange cuvette (0.5 L volume) continuously flushed with a constant flow (400 mL min^{-1}) of VOC-free synthetic air containing 79% N_2, 21% O_2, and 400 ppm of CO_2 mixed from pure gas cylinders (Nippon gases) by means of mass flow controllers (Bronkhorst), and humidified through the headspace of a small tank containing water (Figure 1). The cuvette was placed under a white light metal halide bulb (Osram) at a constant light flux (150 µmol photons m^{-2} s^{-1}). This light flux was previously adjusted in preliminary experiments by measuring the maximum electron transport rate of the bryophyte species. The air temperature was measured with a thermocouple placed inside the cuvette both at the beginning and the end of each experiment and monitored to be 25 ± 2°C throughout the entire experiment. Under all different experimental conditions, the fast air turnover time avoided the build-up of humidity within the cuvette. This was further confirmed by the application of the equation described by Marynick & Marynick (1975), which indicated that only 9% of the original air was present 3 min after flushing the cuvette with an airflow of 400 mL min^{-1}.

Three different and consecutive treatments were applied (Figure 1): **Treatment 1,** hereinafter referred to as control treatment (C). Bryophyte canopies were kept in well-hydrated conditions by flushing the gas exchange cuvette with fully humidified air before time zero (T0), i.e. when desiccation started. **Treatment 2,** referred to as dehydration treatment (Dh). The conditions of desiccation were tested in a pilot experiment before carrying out the real one. The bryophyte canopies were desiccated by flushing the gas exchange cuvette with dry synthetic air (at 0% RH and vapour pressure deficit = 3.17 kPa) at the same rate (400 mL min^{-1}) and air quality (VOC-free synthetic air containing 79% N_2, 21% O_2, and 400 ppm of CO_2 mixed; as described above) obtained by bypassing the tank containing water. The Dh treatment was stopped when the water loss from the bryophyte canopies was stable (i.e. when the slope of the water loss curve was close to 0, i.e. after around 50, 60 and 90 min from T0 in *V. dubyana*, *P. platyphylla* and *P. squarrosa*, respectively). During the dehydration process, the environmental conditions of temperature, light, and air RH%(were kept the same for all species (as specified above). **Treatment 3**, referred to as the rehydration treatment (Rh). Desiccated bryophyte canopies were temporarily removed from the cuvette and fully rehydrated by spraying them with distilled water (≈ 20 mL) for 10 s. The excess water was removed from the surface with a paper towel by using a drip-dry technique that did not damage the leaf tissues (Proctor, 2001; Wang & Bader, 2018). Then, the rehydrated bryophytes were placed back into the cuvette for gas exchange measurements, starting 60 min after T0.

At the end of each treatment (C, Dh and Rh), biomass, relative water content and chlorophyll *a* fluorescence were measured (details below). Besides, for the analysis of both absolute amounts and relative abundance of VTs, the aboveground part of the bryophyte gametophytes (1–3 cm depending on the species and corresponding to ≈ 0.2 g) was cut, cleaned of any debris, frozen instantly in liquid nitrogen and stored at −80°C until VT analysis. Gametophyte is the most dominant, longer-lived part of the

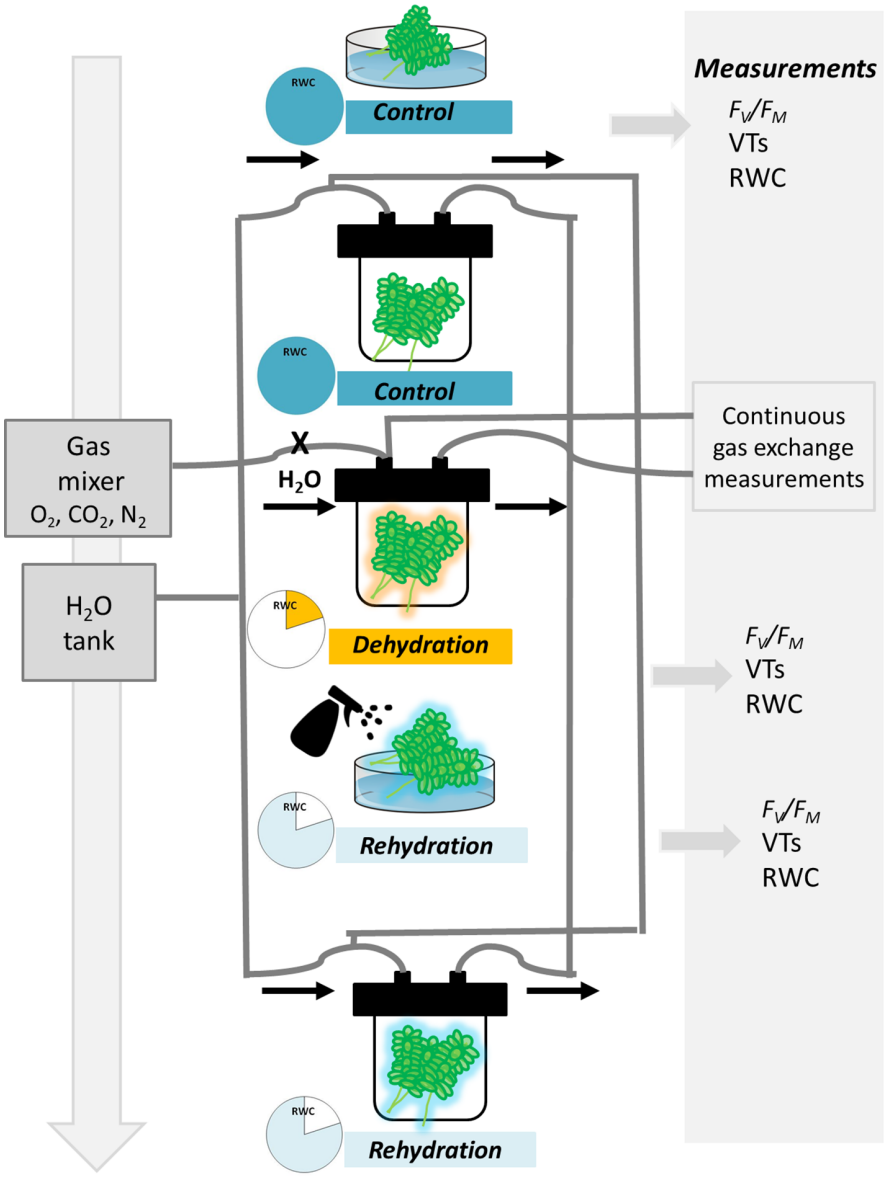

FIGURE 1 Schematic representation of the experimental design to simulate desiccation and rehydration processes. The grey arrow on the left indicates the direction of the consecutive treatments. Desiccation was achieved by bypassing the headspace of the tank containing water so that dry synthetic air flowed through the cuvette. Arrows indicate the direction of the flow. After desiccation, the bryophyte canopies were removed from the cuvette and rehydrated by spraying them with distilled water, as explained in the Materials and Methods section. Afterward, the bryophytes were placed back into the cuvette for gas exchange measurements. Relative water content (RWC) and photochemical efficiency (F_V/F_M) were recorded at three different time points: before the beginning of the experiment (control; from time = −30 min to 0 min), after dehydration (DH, time = 0 min to 50–90 min), and after rehydration (from the end of Dh treatments onwards). In parallel with these determinations, VT samples were collected at these three points for further analysis. Note that to ensure a water loss close to zero each species was subject to different times of desiccation (see Materials and Methods section for more details).

bryophyte's life cycle and consists of a main stem (caulidium) with thin leaves (phyllidia) (Figure 1).

2.3 | Biomass and relative water content determination

Fresh weight (FW) was recorded at three time points: before the beginning of the experiment (Control; FW_C), after Dh (FW_{Dh}), and after rehydration (FW_{Rh}), by weighing plant samples with a 0.1 mg precision balance (A120S, Sartorious, Gottingen, Germany). We considered the FW_C as the turgid weight (RWC = 100%) because the bryophytes were fully hydrated at the beginning of the experiment. To obtain the dry weight (DW), the plant material was dried out at 70°C in an oven for 48 h and samples remained in an airtight jar with silica gel until weighing (to avoid rehydration of the desiccated tissues). The RWC (%) for the different treatments was then calculated as RWC = ((FW-DW)/(FWc-DW))*100, where FW was FW_C, FW_{Dh} and FW_{Rh} in the different treatments.

2.4 | Chlorophyll a fluorescence measurements

Given the spatial heterogeneities of bryophytes, chlorophyll *a* fluorescence was measured at room temperature as a proxy of bryophyte viability on different spots of the canopies using an Imaging Pam M-series fluorometer (Walz). The bryophytes were dark-adapted for 30 min before the measurement. The maximum quantum efficiency of photosystem II (F_V/F_M) was calculated as $(F_M - F_0)/F_M$, with F_0 being the minimum fluorescence and F_M the maximum fluorescence measured after the application of a saturating light pulse of 2600 µmol photons m^{-2} s^{-1}. The maximum value of F_V/F_M in bryophytes has been reported to be lower ($F_V/F_M \sim 0.70$; Hájek and Vicherová 2014, López-Pozo et al. 2019) than in vascular plants

($F_V/F_M \sim 0.83$; Murchie and Lawson 2013). Since the F_V/F_M values that we measured in all our bryophyte samples under fully hydrated conditions were close to the maximum value (= ~0.70; Figure 3), we concluded that all three species successfully acclimated to the laboratory growth conditions and no stress occurred before application of our treatments.

2.5 | Gas exchange measurements

During the experiment, the CO_2 and H_2O exchanges were continuously and simultaneously measured both in the air entering and exiting the cuvette containing the bryophyte species with an LI-7000 infrared gas analyser (Li-Cor Inc.) in differential mode. To assess cuvette airtightness, we checked that the inlet and outlet flow rates were equal when the cuvette was empty. According to Gimeno et al. (2017), either A in the light or Rd in the dark were calculated as:

$$A \text{ or } Rd = F^* \left([CO_2]_{in} - [CO_2]_{out}\right)/DW$$

where F is the flow rate (400 mL min^{-1}), $[CO_2]_{in}$ and $[CO_2]_{out}$ are the CO_2 mixing ratios (μmol mol^{-1}) in the inlet and outlet air, and DW is the dry weight of the canopy (Kg). A was also measured under non-photorespiratory conditions by reducing the O_2 concentration in the inlet air reaching the cuvette from 21 to 2% while CO_2 concentration was maintained steady at 400 ppm. A and Rd were measured under steady-state conditions, at least 15 min after switching the light on and off, respectively. Fast air turnover within the cuvette prevented the excessive accumulation of humidity and water condensation within the tubing, which could have caused the absorption of CO_2. Water loss was also calculated as the difference between the H_2O mixing ratios (mmol mol^{-1}) in the inlet and outlet air, further normalized for the H_2O mixing ratio measured before dehydration started.

2.6 | Analysis and quantification of volatile terpenes

Analysis of VTs (monoterpenes and sesquiterpenes) was performed following the method of Dani et al. (2021) and Marini et al. (2022). Briefly, the samples (previously weighed) were placed in 1.5 mL vials and extracted with 1 mL of heptane. Then the samples were vortexed, mixed and incubated in an ultrasonic bath (BandelinSonorex Super RK 102H) for 15 min three times and successively incubated at 25°C with a rotary shaker plate system (Gerhardt Thermoshake) at 100 rpm for 24 h. The extracted samples were centrifuged at 2500 g for 10 min. Finally, 1 μL of the supernatant (heptane phase) was injected into the gas chromatograph-mass spectrometer (GC–MS) for analysis in a split/splitless injector operating in splitless mode. For GC–MS analysis, an Agilent 7820 Gas Chromatograph system equipped with a 5977E MSD with EI ionization was employed (Agilent Tech.). A Gerstel MPS2 XL autosampler equipped with a liquid option was used. The chromatographic settings were as follows: injector in the splitless mode set at 260°C, J&W Innovax column (30 m, 0.25 mm i.d., 0.5 μm df); oven temperature program: initial temperature 40°C for 1 min, then a ramp of 5°C min^{-1} until 200°C, then a ramp of 10°C min^{-1} until 220°C, then a ramp of 30°C min^{-1} until 260°C, and a final hold time at 260°C of 3 min. The mass spectrometer was operated with an electron ionisation of 70 eV in scan mode in the m/z range 29–330 at three scans s^{-1}. Here we present results concerning VTs only, albeit several other VOCs were produced in traces. To quantify the different compounds, a calibration curve was constructed by injecting known concentrations of pure high-purity standards obtained from Sigma-Aldrich S.r.l. and Acros (Geel) into the gas chromatograph-mass spectrometer. The deconvoluted VT peak spectra, obtained by Agilent MassHunter software, were matched against the NIST 11 spectral library for tentative identification. Results of the VT analysis are represented by: (1) absolute amounts of VTs (total concentration) calculated as the sum of all VTs detected in each sample and expressed as ng g^{-1} DW; (2) absolute amounts of oxygenated (cineole and δ-carvone) and non-oxygenated (limonene, γ-terpinene, terpinolene, p-cymene, β-pinene, myrcene, α-pinene, α-phellandrene, β-caryophyllene and camphene) VTs based on the presence or absence of oxygen in their molecular structure, with these subcategories being expressed with the same units (ng g^{-1} DW); (3) relative abundance of each VT expressed as a percentage of total VTs (VT profile).

2.7 | Data processing and statistical analysis

Data reported in the figures refer to 3–7 replicates for each treatment and each bryophyte species (each replicate corresponding to a single bryophyte canopy), unless otherwise stated.

Differences in parameters among bryophyte species and treatments (C, Dh and Rh) were compared by a repeated ANOVA measurement with "species" (*Sp*) as the between factor and "treatment" (*Treat*) as the within repeated factor: i.e., RWC; F_V/F_M; A, (under both ambient and low O_2 conditions); Rd; absolute amounts of VTs (total, oxygenated and non-oxygenated). The interaction factor between *Sp* and *Treat* was also assessed (Sp x Treat). Then, a post-hoc analysis using the Bonferroni multiple testing correction method was performed to reveal pairwise statistical differences between treatments. All data were tested for normality (Kolmogorov–Smirnof test), with the assumption of sphericity (Mauchly's test) and homogeneity of variances (Cochran test). Non-normally distributed variables were normalized by log transformation. We used a non-metric multidimensional scaling (NMDS) to visualize VT variation across treatments and bryophyte species by an Euclidean distance matrix based on VT relative abundance, using the metaMDS function of the *vegan* package (Jari Oksanen et al., 2019). To compare and test the null hypothesis of no difference in VT relative abundance composition between

bryophyte species and different treatments, we used permutational MANOVA (PERMANOVA), which is a permutation-based multivariate ANOVA employed to test the effect of treatments on a response of many variables (e.g. VTs; Anderson, 2001) using the adonis function of the *vegan* package (Jari Oksanen et al., 2019). The Euclidean distance on VT relative abundances was used as a response matrix, and species (*P. platyphylla*, *P. squarrosa and V. dubyana*), treatment (C, Dh, Rh), and their interaction were used as explanatory factors. Since treatments were applied to the same individual sample of bryophytes over time, this was included as strata in adonis, to account for the repeated measures design. *P*-values were computed using 999 permutations. Finally, VT abundances, scaled to unit variance, of each compound in specific species and treatment combinations were visualized using a heatmap constructed with the ggplot2 package in R (Wickham, 2016). The statistical tests were considered significant at $\alpha = 0.05$. Statistical analyses were performed with IBM SPSS Statistics for Windows, Version 24.0. (IBM Corp.) and R (R Core Team, 2020).

3 | RESULTS

3.1 | RWC and chlorophyll a fluorescence

The three bryophyte species were fully hydrated before the start of the experiments (RWC 100%; Figure 2), and the values of F_V/F_M were = 0.68 ± 0.02, 0.67 ± 0.02 and 0.63 ± 0.02 for *P. squarrosa*, *P. platyphylla* and *V. dubyana*, respectively (Figure 3).

Dehydration decreased the RWC values to ~20% in both *P. squarrosa* and *P. platyphylla* (Figure 2a, b), and to ~5% in *V. dubyana* (Figure 2c). F_V/F_M also significantly decreased during dehydration: values recorded in the Dh bryophytes were: 0.52 ± 0.02 in *P. squarrosa* and 0.53 ± 0.04 in *P. platyphylla*, whereas a much lower F_V/F_M (0.34 ± 0.02) was observed in *V. dubyana* (Figure 3).

The Rh treatment resulted in a rapid recovery of RWC to ~100% of the initial values in both *P. squarrosa* and *P. platyphylla* (Figures 2a, b), and ~ 80% in *V. dubyana* (Figure 2c). After Rh, the F_V/F_M values recovered quickly to control values in the DT species *P. squarrosa* and *P. platyphylla*, whereas the DS species *V. dubyana* showed an even lower F_V/F_M than observed in Dh conditions (Figure 3).

3.2 | Photosynthesis (under normoxic and hypoxic conditions) and dark respiration

Before dehydration, A was 11.3 ± 3.8, 19.7 ± 3.6, and 105.8 ± 5.8 μmol CO_2 kg^{-1} DW s^{-1} in *P. squarrosa* (Figure 5a), *P. platyphylla* (Figure 5b) and *V. dubyana* (Figure 5c), respectively. Time courses of A and water loss during the Dh treatment (Figure 4) showed that A and water loss decreased similarly during the desiccation period in the two DT species (but faster in *P. platyphylla*; Figure 4a, c). An even steeper decrease was observed for *V. dubyana*, where values close to 0 were reached by the end of the Dh period for both A and water loss (Figure 4e, f). Photosynthesis recovered to 81 and 43% of the initial values in the two rehydrated DT species (Figure 5 a, b), whereas no recovery was observed in the DS *V. dubyana* (Figure 5c).

Before dehydration, photorespiration was measurable in all species, as A increased under low O_2 and non-photorespiratory conditions, with respect to A observed in ambient air (Figure 5). When exposed to Dh under non-photorespiratory conditions, A remained unchanged in *P. squarrosa* (Figure 5a), decreased in *P. platyphylla* (Figure 5b) and decreased further in *V. dubyana*. In the DS species, A did not increase again after rehydration, even under non-photorespiratory conditions (Figure 5c).

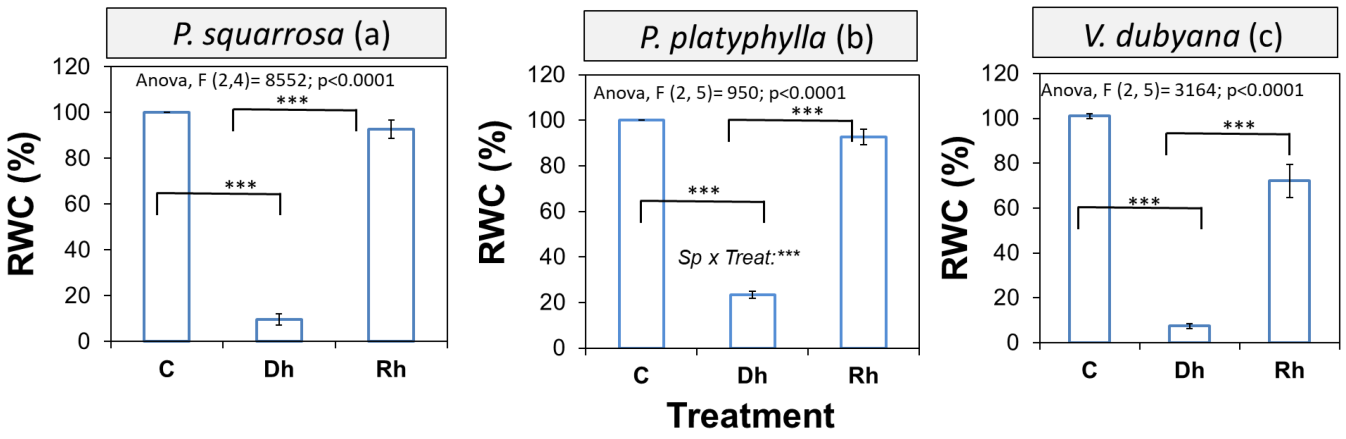

FIGURE 2 Treatment response of the relative water content (RWC; %) for the three bryophytes: *P. squarrosa* (a) *P. platyphylla* (b), and *V. dubyana* (c). Three treatments were applied as explained in Figure 1: Control (C) dehydration (Dh) and rehydration (Rh). Values are the means of 3–7 replicates ± standard error (SE). Differences in RWC among species and sampling time treatments (C, Dh and Rh) were compared using a repeated ANOVA measurement with "species" as the between factor and "treatment time" as the within repeated factor. The interaction factor for the species (*Sp.*) and treatment (*Treat*) was also assessed. Post-hoc analyses with a Bonferroni test revealed the pairwise statistical differences between time points (***$P < 0.001$).

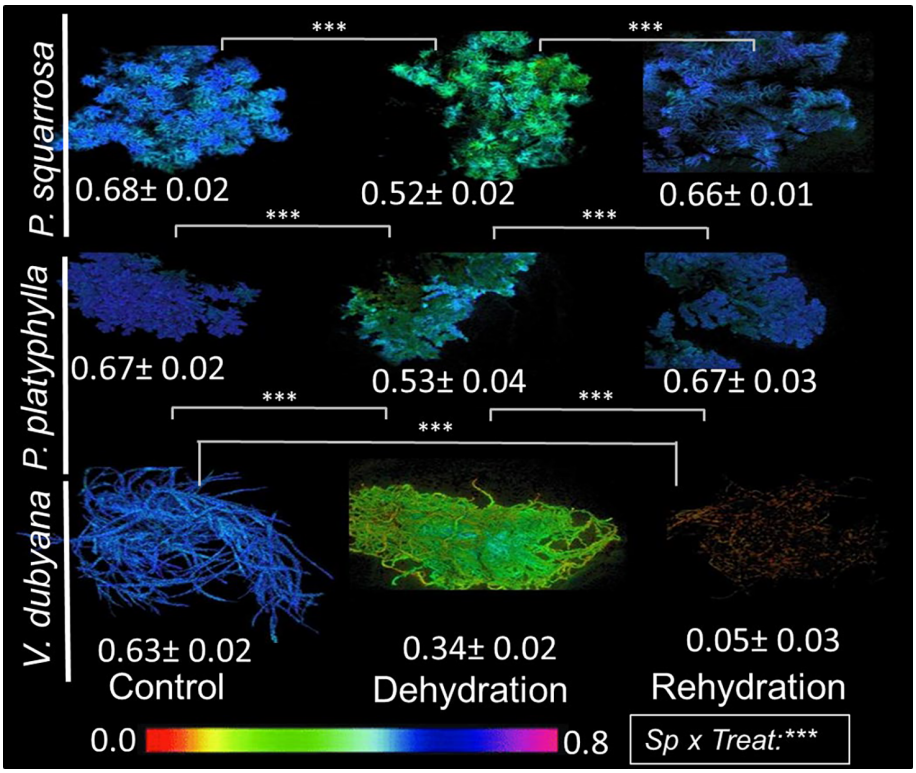

FIGURE 3 Treatment response of the maximum quantum efficiency of PSII (F_V/F_M) for the three bryophytes: *P. squarrosa* (a) *P. platyphylla* (b), and *V. dubyana* (c), after 15 min dark-adaption. Three treatments were applied as explained in Figure 1: Control (C); dehydration (Dh) and rehydration (Rh). False-colour images show representative measurements of F_V/F_M collected from the three studied species (from F_V/F_M 0 to 0.8). Values are mean of 3–7 replicates ± SE. Differences in F_V/F_M among species and sampling time treatments (C, Dh and Rh) were compared using a repeated ANOVA measurement with "species" as the between factor and "treatment time" as the within repeated factor. The interaction factor for the species (*Sp*) and treatment (*Treat*) was also assessed. Post hoc Bonferroni tests revealed the pairwise statistical differences between time points (***P < 0.001).

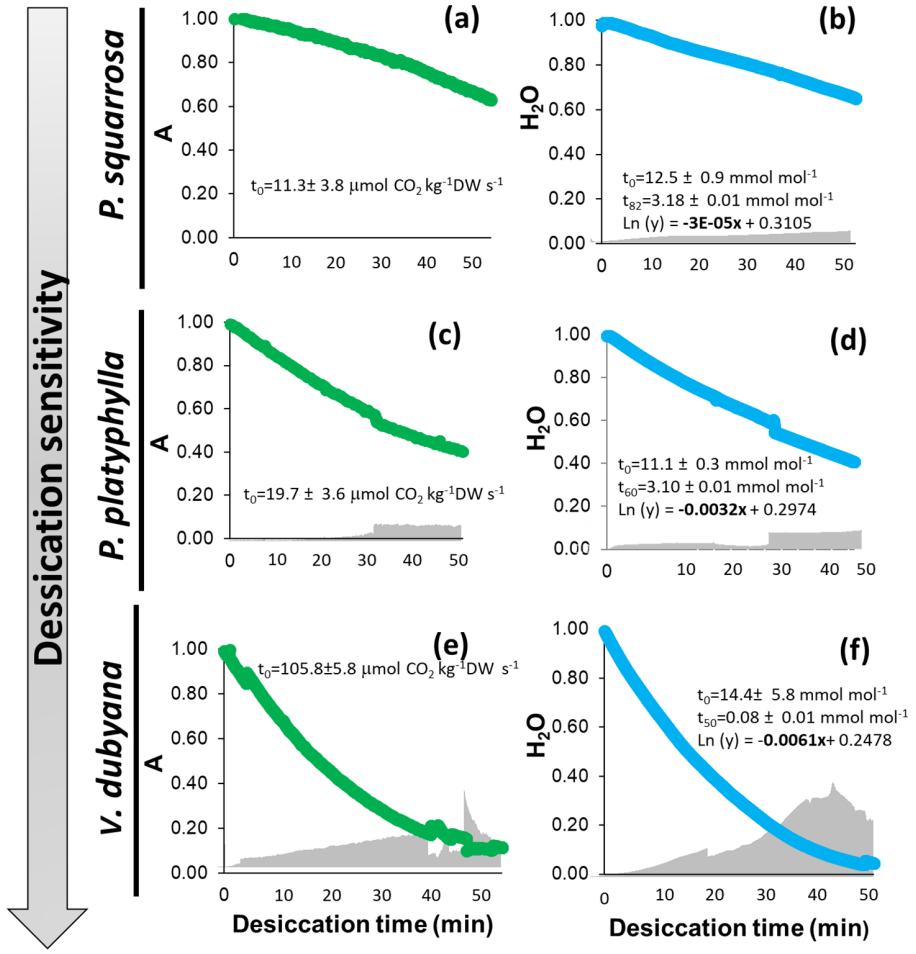

FIGURE 4 Normalized photosynthetic assimilation rate (A) and water loss (H_2O) upon desiccation monitored continuously for 50 min in *P. squarrosa* (a, b), *P. platyphylla* (c, d) and *V. dubyana* (e, f). The arrow in the left part of the figure indicates the degree of desiccation sensitivity of the species (determined by previous experiments). The function for each parameter for water loss is shown in the figure inset. Values are means of 3–7 replicates. Standard error (SE) with respect to the mean values is shown in grey.

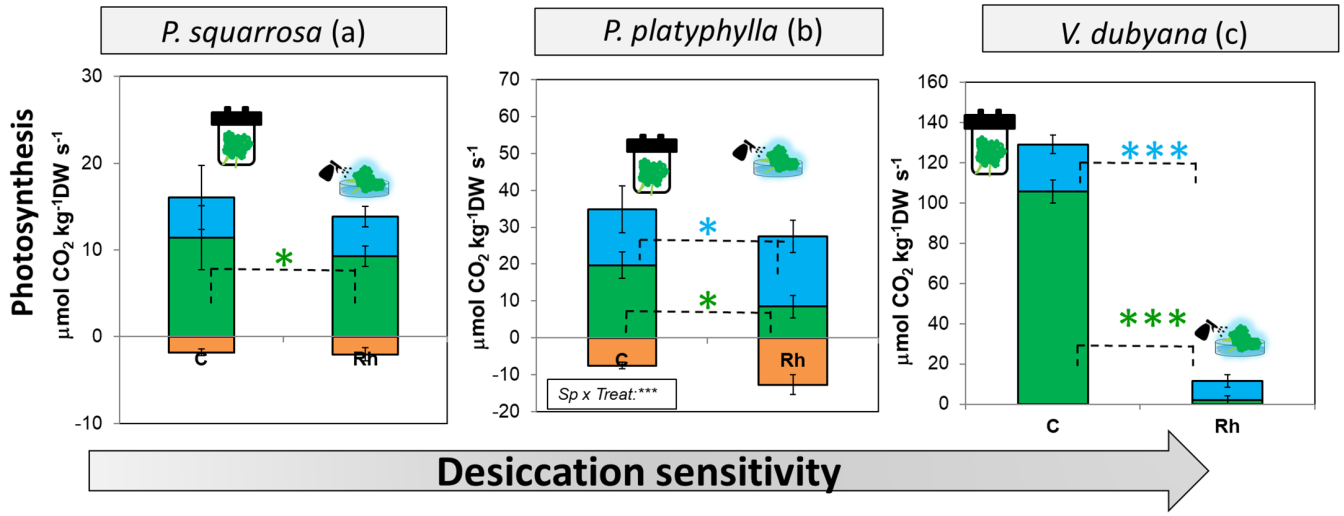

FIGURE 5 Fluxes (µmol CO_2 kg^{-1} DW s^{-1}) of CO_2 assimilation under 20% O_2 (normoxic conditions; green bars), under 2% O_2 (*hypoxic* conditions; green-blue bars together) and respiration (orange bars) before desiccation (C) and after rehydration (Rh) in *P. squarrosa* (a), *P. platyphylla* (b) and *V. dubyana* (c). The arrow in the lower part of the figure indicates the degree of desiccation sensitivity of the species (determined by previous experiments). Data are presented as the means of 3–7 replicates ± standard error (SE). The interaction factor between the species and treatment was also assessed. Post hoc Bonferroni tests revealed the pairwise statistical differences between time points (*P < 0.05; ***P < 0.001).

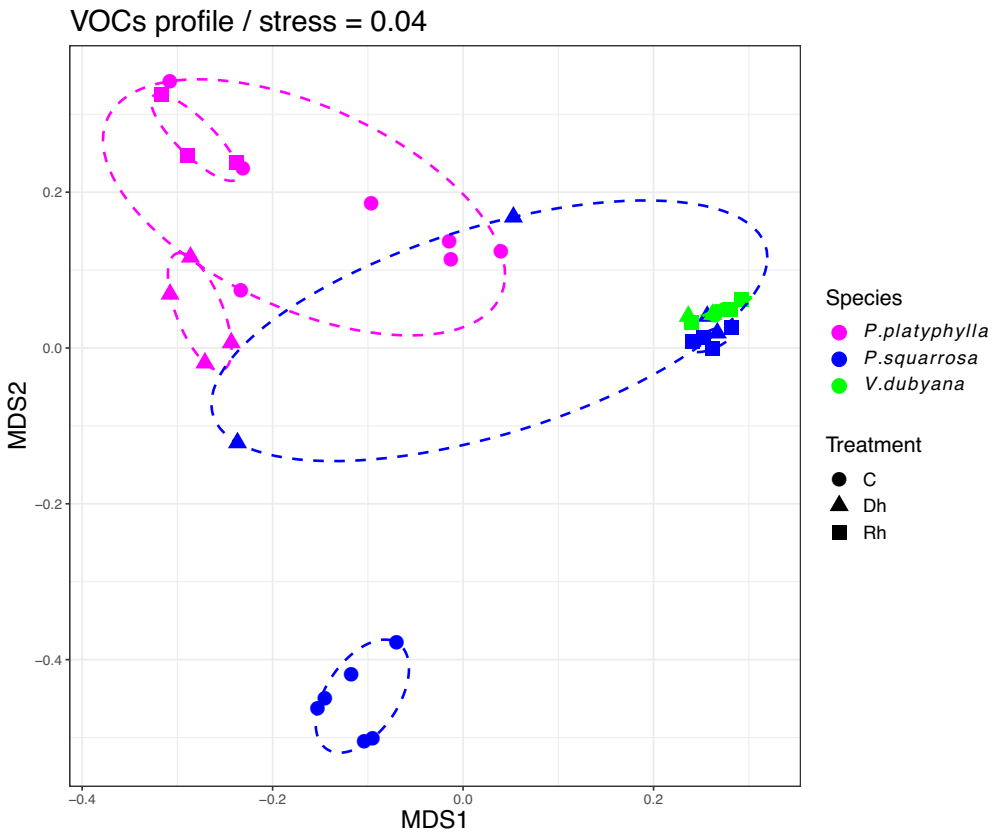

FIGURE 6 Non-metric multidimensional scaling (NMDS) ordination (stress value = 0.04) of the bryophyte samples according to their VT profiles: *P. squarrosa*, *P. platyphylla*, and *V. dubyana*. Colours depict bryophyte species, whereas shapes indicate different treatments: control (C), dehydration (Dh) and rehydration (Rh). Ellipses show clustering of the samples of the same species and treatment.

The Rd remained constant in rehydrated *P. squarrosa* and *P. platyphylla* compared to controls (Figures 5a, b), whereas Rd was very low and could not be measured in *V. dubyana* (Figure 5c).

3.3 | Volatile terpenes

The NMDS plot based on VT relative abundance revealed the level of similarity between the VT content in the three bryophyte species

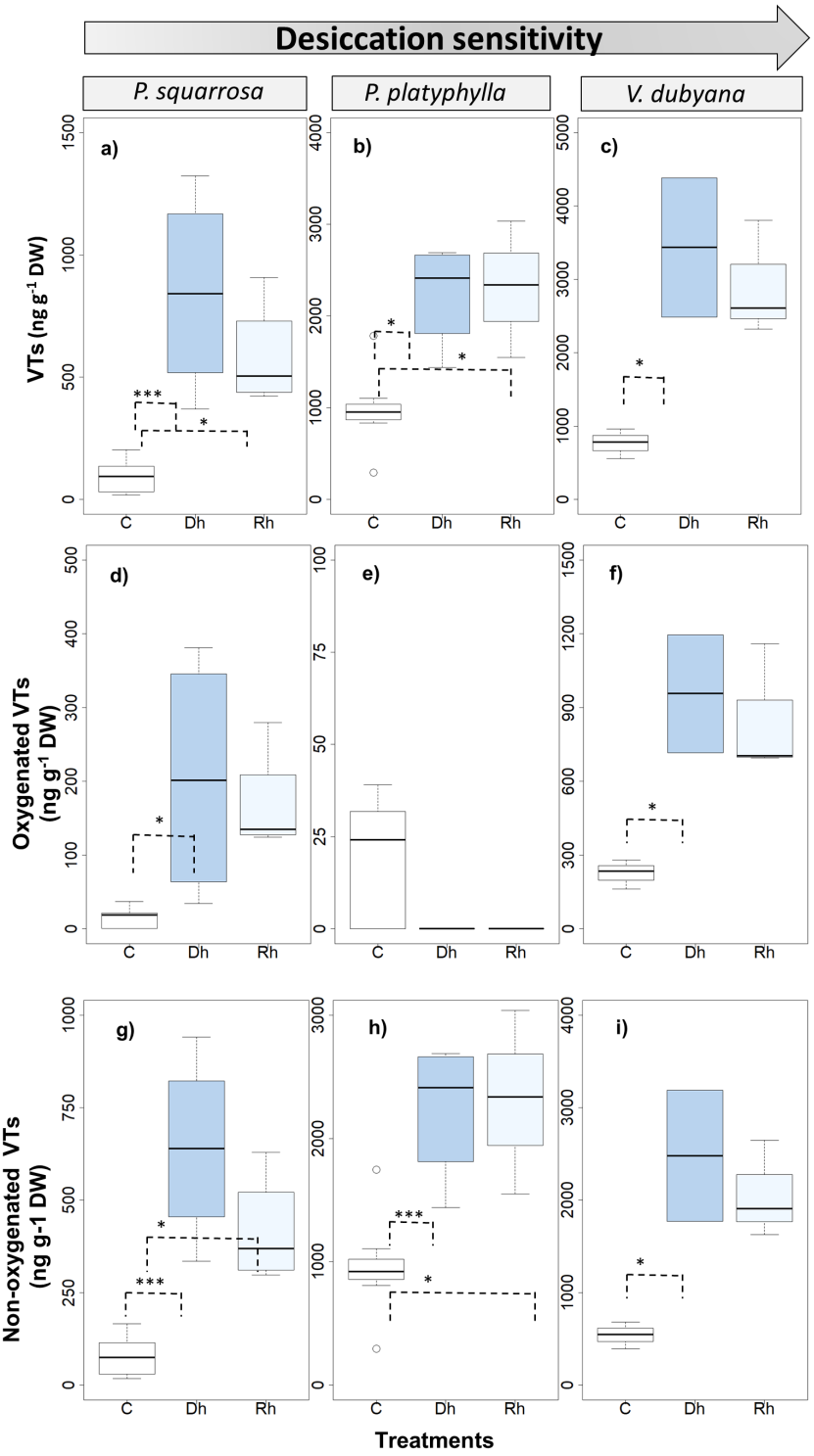

FIGURE 7 Boxplots showing the absolute, oxygenated and non-oxygenated amount of the total pool of VTs (ng g^{-1} DW) in the three bryophyte species: *P. squarrosa* (a, d, g) *P. platyphylla* (b, e, h), and *V. dubyana* (c, f, i), in control conditions (C), and after dehydration (Dh) and rehydration (Rh). The arrow in the upper part of the figure indicates the level of desiccation sensitivity of the species (determined by previous experiments). Central lines represent the medians and whiskers represent the minimum and maximum values (n = 2–7). The interaction factor between the species (*Sp.*) and treatment (*Treat*) was also assessed and was significant ($p < 0.001$). Post hoc Bonferroni tests revealed the pairwise statistical differences between time points (*P < 0.05, ***P < 0.001).

under C, Dh and Rh treatments (Figure 6; Table S1). In particular, VTs were significantly species-specific (PERMANOVA, $Df_{nom} = 2$, $Df_{den} = 27 R^2 = 0.53$, p-value = 0.001) and, to a lesser extent, reacted similarly to the treatment (PERMANOVA, $Df_{nom} = 2$, $Df_{den} = 27$, $R^2 = 0.08$, p-value = 0.006). Moreover, significant species × treatment interaction (PERMANOVA, $Df_{nom} = 4$, $Df_{den} = 27$, $R^2 = 0.25$, p-value = 0.001) indicated that the effect of treatment on VTs depended on the bryophyte species (Figure 6). Under C conditions, we found minor clustering between bryophytes, meaning that VT relative abundance was different in the three bryophyte species when fully hydrated. After the Dh treatment, relative VT abundance was separated from their respective controls in *P. squarrosa* and *P. platyphylla* but not in *V. dubyana* (Figure 6). After Rh, the VT relative abundance again tended to align with that of controls in the case of *P. platyphylla*, whereas in *P. squarrosa* rehydrated samples remained separated from the controls (Figure 6).

The total absolute amounts of VTs were analysed in the three bryophyte species under C, Dh and Rh conditions (Figure 7a-c). The initial absolute VT pool in C conditions largely and significantly ($p < 0.05$) varied between the three bryophyte species, being lower in *P. squarrosa* (92.7 ± 26.5 ng g^{-1}DW; Figure 7a) than in both *P. platyphylla* (977.7 ± 166.5 ng g^{-1}DW; Figure 7b) and *V. dubyana* (765.6 ± 117.5 ng g^{-1}DW; Figure 7c). In response to Dh, the total content of VTs increased in the three species (compared to the values at C), and was independent of the degree of desiccation tolerance (Figure 7a-c). In fact, this increase was nine-fold in the DT *P. squarrosa* (Figure 7a; from 92.6 ± 23.3 ng g^{-1}DW to 843.3 ± 137.9 ng g^{-1}DW), but only 4-fold in the DS *V. dubyana* (Figure 7c; from 977.7 ± 67.8 ng g^{-1}DW to 2237.7 ± 446.1 ng g^{-1}DW), and 2-fold in the other DT *P. platyphylla* (Figure 7b; from 765.6 ± 155.8 ng g^{-1}DW to 3435.0 ± 193.0 ng g^{-1} DW). After Rh, the VT content remained as high as during Dh in the three species (Figure 7a-c).

When we grouped the VTs (absolute amounts) in oxygenated and non-oxygenated compounds, the latter, making most of the total VTs, were found to be enhanced in all dehydrated samples (Figure 7g, h, i). However, oxygenated VTs (cineole+ δ-carvone) returned to the low level of C after Rh treatment in *P. platyphylla* (Figure 7e), while behaving similarly to total and non-oxygenated VTs in the mosses (*P. squarrosa*, Figure 7d and *V. dubyana*; Figure 7f).

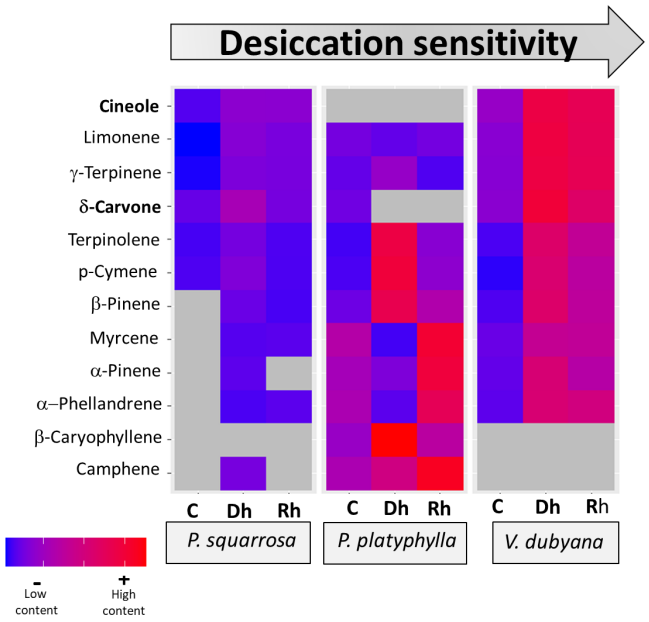

FIGURE 8 Heatmap highlighting the abundances (scaled to unit variance) of VTs measured in each of the bryophyte species (*P. squarrosa*, *P. platyphylla* and *V. dubyana*) and in the treatments applied (Control, C; Dehydration, Dh, and Rehydration, Rh). The rows represent the VTs and the columns represent the species under the different treatments. The intensity of the colour of the heatmap (from blue to red) is relative to the VT contents (from low to high values), whereas grey indicates that the VT was not present. The compounds in bold are oxygenated VTs. The arrow in the upper part of the figure indicates the degree of desiccation sensitivity of the species (determined by previous experiments).

The changes in the abundance of VTs (scaled to unit variance) after dehydration and rehydration were also analysed by generating a heatmap graphical depiction (2-D matrix) for each compound (Figure 8). Overall, this map showed different patterns of individual VTs depending on the treatment and the species. Comparing the changes from the control condition to Dh and Rh, the greatest colour range changes (from blue to red) characterized the DS species *V. dubyana*. Here, the content of most VTs (e.g. cineole, limonene, γ-terpinene, δ-carvone, terpinolene, p-cymene, β-pynene, myrcene, α-pynene, α-phellandrene) increased with Dh and was stable or slightly decreased again with Rh (Figure 8). Besides, β-caryophyllene and camphene were not found in *V. dubyana*. In *P. platyphylla*, which showed higher desiccation tolerance than *V. dubyana*, high contents of myrcene, α-pinene, α-phellandrene were found in control conditions, but these VTs decreased during Dh and increased again after Rh (Figure 8). Other VTs, like γ-terpinene, terpinolene, p-cymene, β-pinene, β-caryophyllene showed the opposite trend in this species as they increased following Dh and decreased again upon Rh. The monoterpene camphene increased during Dh and continued increasing in Rh. In *P. platyphylla*, we did not find δ-carvone in Dh and Rh and the monoterpene cineole was not found in any of the treatments (Figure 8). Finally, in *P. squarrosa*, which was the species with the lowest absolute amount of VTs (Figure 7b) but the highest DT (Figures 2 and 3), the main VTs (limonene, δ-carvone, terpinolene, p-cymene) increased after Dh and decreased again after Rh. By contrast, cineole, γ-tepinene, myrcene, α-phellandrene and camphene increased upon Dh and subsequent Rh. We did not find the sesquiterpene β-caryophyllene in this species under any treatment, whereas the monoterpenes β-pinene, myrcene, α-pinene, α-phellandrene were not found in the C treatment. However, these same monoterpenes increased to a measurable amount after the Dh treatment in *P. squarrosa*.

4 | DISCUSSION

4.1 | Bryophytes with different sensitivities to desiccation also showed different photosynthesis

Our experiments, which were designed following the criteria of Stark (2017), confirmed the classification of the three bryophyte species regarding desiccation sensitivity based on their ecological attributes (Hill et al., 2007; López-Pozo et al., 2019). Indeed, we found a desiccation sensitivity gradient in the species analysed: *V. dubyana* (aquatic, thus DS), *P. platyphylla* (from semi-shaded well-drained sites, and accordingly moderately DT) and *P. squarrosa* (growing in full light and dry environments, thus DT). We highlight that when comparing *V. dubyana* (DS) with the other two species *P. platyphylla* and *P. squarrosa*, the DS species: (1) lost water more rapidly during dehydration and did not fully recover RWC after Rh (Figure 2). The faster loss of water of *V.dubyana* may depend on several factors (Pammenter et al., 2002), such as the hydraulic conductivity of the

tissues (which is affected by the presence of physical barriers in the outer layers; Buda et al., 2013), and the shoot architecture and higher surface area (i.e., phyllids are thinner in *V. dubyana* than in *P. platyphylla* and *P. squarrosa*); (2) substantially and irreversibly reduced photochemical efficiency, as revealed by chlorophyll fluorescence ($F_V/F_M = 0.05$ after Rh; Figure 3); (3) showed a more rapid and complete drop in A during Dh (Figure 4); and (4) did not recover initial A values after Rh (Figure 5). Moreover, the DS species *V. dubyana* has intrinsically higher A (in well-watered control conditions) than the other two tolerant species (*P. platyphylla* followed by *P. squarrosa*; Figure 4; Figure 5). Indeed, bryophytes have the lowest A amongst terrestrial plants (Flexas & Carriquí, 2020), and photosynthetic rates increase from bryophytes to angiosperms (i.e. bryophytes, lycophytes, pteridophytes and spermatophytes) under non-stressful growth conditions (Marschall & Proctor 2004, Hanson et al., 2014, Flexas & Gago 2018, Carriquí et al., 2019). The low A in bryophytes has been related to morphological constraints to CO_2 diffusion (i.e. lower CO_2 conductance), mainly because of the large cell wall thickness of these plants (Carriqui et al., 2019) and/ or to reduced ribulose-1,-5-bisphosphate carboxylase-oxygenase (RuBisCO) protein content (Galmés et al., 2014) indicating high biochemical limitations (Perera-Castro et al., 2022). However, a large intrinsic variation in photosynthetic capacity exists among bryophytes, likely associated with differences in the morphology of the photosynthetic tissues (Hanson et al., 2014). This explains why mosses belonging to the *Polytrichum* genus can reach high photosynthetic rates comparable to those of some angiosperms (Carriquí et al., 2019). At the same time, the observation of very high A in *V. dubyana* under optimum hydration (Figure 5) implies that high photosynthetic rates in bryophytes are often inversely associated with stress resistance. Indeed, desiccation tolerance is tightly linked to low A in bryophytes (Alpert, 2006; Proctor et al., 2007), similar to what was observed in seed plants (e.g. Loreto et al., 2003). The anatomy-mediated trade-off between A and desiccation tolerance (Flexas & Gago, 2018) could explain the lower A of more desiccation-tolerant species (*P. platyphylla* and *P. squarrosa*), because rigid cell walls allowing water conservation may also restrain CO_2 exchange, especially in stomata-free bryophytes. Bryophytes were described as outliers of the A-bulk modulus of the elasticity trade-off (Perera-Castro et al., 2021), which means that high A is not compatible with rigid leaves. This is due to the passive exchange of CO_2 and water vapour through the mesophyll, which is unregulated by stomata. Recently, a larger cell wall porosity (related to elasticity but independent of cell wall thickness) has been claimed to explain the lower A of bryophytes compared to vascular plants (Perera-Castro & Flexas, 2022). On the other hand, a higher A in *V. dubyana* may also be explained by the presence of anatomical traits favouring CO_2 conductance, such as thinner phyllidia (Waite & Sack, 2010). Indeed, under a fully hydrated condition, a film of water covering the interstitial spaces in bryophytes may restrict CO_2 diffusion, thereby limiting photosynthesis (Wagner et al., 2013). However, in aquatic bryophytes, such as *V. dubyana*, this limitation might be relieved by an unknown CO_2 concentrating mechanism or/and by the use of bicarbonate as a carbon source (Glime, 2014).

Consistent with previous studies, the photosynthetic response in the investigated bryophyte species was greatly affected by Dh (Figures 4, 5, Challabathula et al., 2018), due to the extreme water dependence of these organisms (Alpert, 2000; Proctor, 2000). The drop in photosynthesis during dehydration has been explained by a reduction in the activity of the Calvin cycle enzymes (e.g. RuBisCO or chloroplastic GAPDH; de Carvalho et al. 2011; Cui et al. 2012). The lack of both stomata and cuticle explains the concomitant and rapid decrease in water content (Figure 2; Flores-Bavestrello et al., 2016; Niinemets et al., 2018), and thus the decrease in A during Dh (Perera-Castro et al., 2021). However, when exposed to the same standardized desiccation protocol, a more intense water loss occurred in *V. dubyana* than in the two more desiccation-tolerant species *P. platyphylla* and *P. squarrosa* (Figure 4), leading to higher stress on photosystem II and thus stronger metabolic impairment (Figures 3, 5), from which *V. dubyana* was unable to recover. Instead, rehydration resulted in a partial recovery of A in *P. platyphylla* and *P. squarrosa* (Figures 3, 5). Rd also restarted quickly upon rehydration in these two species (Figure 5; Proctor et al., 2007b), reaching values higher than in control. Recovery of both A and Rd in *P. platyphylla* and *P. squarrosa* confirmed the desiccation tolerance of these two species, possibly via a mechanism compatible with the homoichlorophyllous strategy that maintains the integrity of the photosynthetic apparatus during desiccation in resurrection plants (Gao et al., 2017, Proctor 2001).

We also observed in all the species an increase in A under non-photorespiratory conditions (Figure 5; <2% O_2), which is comparable to or even higher than the increase reported in seed plants. Thus, RuBisCO also acts both as a carboxylase and oxygenase enzyme in bryophytes. Comparative studies from liverworts to ferns, to gymnosperms and throughout angiosperms have indicated increasing rates of photorespiration during evolution (Hanawa et al., 2017). Photorespiration is considered an important stress protection mechanism (Wingler et al., 2000), serving as a dissipative energy process that acts as a safety valve and being generally associated with the prevention of ROS accumulation. In particular, photorespiration has been shown to increase and become the main electron sink under A suppression in the bryophytes *Marchantia polymorpha* and *Conocephalum conicum* (Hanawa et al., 2017), thus indicating a high capacity for oxygen photoreduction when CO_2 assimilation is limited (Proctor & Smirnoff 2011). Recently, it was also shown that photorespiration in the moss *Sphagnum* was modulated by water table content and CO_2 atmospheric levels, being suppressed under low water table and elevated CO_2 (Serk et al., 2021). In our experiment, we expected a greater increase in A under non-photorespiratory conditions when limited by low O_2 availability during dehydration. However, this occurred only in *P. platyphylla*. Low stimulation of A under non-photorespiratory conditions may reveal the onset of biochemical limitations (RuBisCo deactivation) in severely dehydrated samples, especially in *V. dubyana*, where A could not be restored after rehydration.

The third component of CO_2 gas exchange is Rd, which is much lower than photosynthesis and photorespiration. However, it has

been reported that Rd rates are higher in bryophytes than in other terrestrial plant groups (e.g. Wang et al., 2017; Carriquí et al., 2019). We have also found high rates of Rd relative to A in the more desiccation-tolerant species (*P. squarrosa* and *P. platyphylla*), which could imply higher maintenance costs (i.e., more nitrogen allocation to photosynthetic components), especially after dehydration (Fan et al., 2020; Waite & Sack, 2010) in these bryophyte species. Low respiration is generally associated with high photosynthetic rates in plants that recycle substantial proportions of respiratory CO_2 (Loreto et al., 2001; Pinelli & Loreto 2003), and this may also be the case for bryophytes. Consistently, Rd was not measurable in *V. dubyana*, where it was too low and below our detection limit. Alternatively, a concentrating CO_2 mechanism may be present in aquatic bryophytes that prevent Rd detection (Glime, 2014). The absence of the maintenance component of Rd might be associated with irreversible impairment of basal metabolism in the dehydrated *V. dubyana*.

4.2 | Volatile terpenes were differently affected by dehydration and rehydration in desiccation-sensitive and tolerant bryophytes

While knowledge of A, photorespiration and Rd in bryophytes has progressed, little information about VOC production by bryophytes can be found (Chen et al., 2018; Vicherová et al., 2020). Bryophytes, especially liverworts, possess oil bodies that have been described to contain mono- and sesquiterpenes, as well as non-volatile diterpenes (Ghani et al., 2016; Linde et al., 2016; Ludwiczuk & Asakawa, 2019). Consistent with previous studies, we found VTs to be the main VOCs in all the three bryophytes we have investigated (Figure 7). In particular, the liverwort species (*P. platyphylla*) was the only one producing a sesquiterpene (β-caryophyllene).

If VT composition in this phylogenetic group has been rarely investigated, even less information is available regarding the response of bryophyte VTs to challenging environmental conditions. VT changes have been studied in response to different light quality (Vicherová et al., 2020), but never when water is deprived (a very frequent environmental stress for these organisms). In woody plant species, a higher monoterpene production is associated with the transition to more xeric habitats (Loreto et al., 2014), and monoterpene-rich plants are better invaders because of their resistance to stresses (Llusià et al., 2010). In bryophytes, the highest monoterpene pool was found in the more desiccation-sensitive species (*V. dubyana*). Although there may be similarities between response to stress in bryophytes and vascular plants (e.g. enhanced pools of antioxidants under stressful situations), the differential physiology of bryophytes (e.g. lack of stomata and vascular tissue), together with their bryological attributes (Hill et al., 2007) and ecological strategies (i.e., life-form, type of perennation, environmental requirements such as light and water), and even their complicated taxonomy (liverwort versus moss) may determine important differences when bryophytes cope with desiccation and other environmental stresses. Indeed, our results (Figure 6) indicated that VTs of bryophytes were more influenced by species than by treatment and varied quantitatively among different treatments and species. Overall, distinctive VT profiles characterized the three bryophyte species under optimum hydration independently of their desiccation tolerance characteristics (Figure 6), as previously described (Linde et al., 2016). However, the total constitutive VTs (mainly monoterpenes) under optimum hydration conditions showed an association with photosynthetic capacity, being both VTs and A highest in the DS *V. dubyana* (Figure 5 and 7). This suggests that also in bryophytes, monoterpenes are synthesized by the photosynthesis-dependent 2-C-methyl-D-erythritol 4-phosphate pathway (Lichtenthaler et al., 1997).

When A declines because of environmental stresses, a higher fraction of photosynthetic carbon and energy is usually allocated to VTs biosynthesis (e.g. Brilli et al., 2007; Niinemets, 2010; Centritto et al.,2011; Haworth et al., 2017), as well as to other protective secondary metabolites. Investment in VT production was also higher in the three bryophytes when A declined because of desiccation but remained high after rehydration (Figure 7). Our results confirm those observed in the resurrection plant *Xerophyta humilis*, where VT (isoprene) production increased with desiccation and remained high after rehydration (Beckett et al., 2012), perhaps helping plants cope with high production of ROS during occurring during both desiccation and rehydration (Beckett et al., 2012; Cruz De Carvalho et al., 2012; Scheibe &Beck, 2011). VTs were also high in *V. dubyana* after exposure to dehydration (Figure 7c). However, we hypothesize that, in this case, the rapidly evolving stress overcame any defensive function of VTs, as shown by the unrecoverable decay of photosynthesis (Figure 5), VTs serve as antioxidants and membrane strengtheners only when the stress is mild and transient, whereas under severe and more persistent stresses plants synthesize less volatile protective compounds (Beckett et al., 2012; Tattini et al., 2015).

Thus far, attention has been directed towards the pool of total VTs (Figure 7a-c). However, a better understanding of VT mechanisms and functions may be attained by analyzing the trends exhibited by individual compounds within this pool. Enhancement of oxygenated monoterpenes (cineole and δ-carvone) in both *P. squarrosa* (Figure 7d) and *V. dubyana* (Figure 7f) following dehydration was observed. An increase of these compounds was reported under elevated temperatures in angiosperms (Okereke et al., 2022; Zuo et al., 2017) and it might be indicative of increased leaf oxidative status and resulting non-enzymatic terpene oxygenation (a possible case for *V. dubyana*), or shifts in monoterpene synthesis, which is operated by different monoterpene synthases, depending on abiotic stress occurrence (probably this is the case for *P. squarrosa*), as shown in other species (Okereke et al., 2022; Pazouki et al., 2016).

In the present experiment, the heatmap (Figure 8) representing changes in the production of individual VTs in the three species in C conditions, after Dh, and after Rh, may help describe patterns of bryophyte responses to the desiccation (treatment). However, it is also possible that the VTs fingerprint is more dependent on the species (genetics) than on VT function. A marked species-specific tolerance has been recently described in bryophytes based on other

(non-volatile) isoprenoid responses (i.e. tocopherols) (De Agostini et al., 2022). We found greater changes in VT abundance (Figure 8; across C, Dh and Rh phases) as the desiccation sensitivity of the species increased (*P. squarrosa* < *P. platyphylla* < *V. dubyana*). Overall, the ecological strategies and environmental requirements (i.e., light and water) of the species used here may help explain the observed VT variability when responding to a desiccation sensitivity gradient. The moss *P. squarrosa* usually occupies light-exposed niches with a dry substrate and is the most DT species, consequently frequently exposed to ROS damage. This species may need less volatile, and more stable isoprenoids with lower metabolic cost (i.e. tocopherols or carotenoids synthesis), and that provide better protection when plants are challenged by severe stress (Fini et al., 2017). Indeed, in the resurrection plant *Xerophyta humilis*, isoprene emission stopped at 5% RWC, and it was replaced by zeaxanthin to enhance membrane stability, being more effective as a protective agent (Beckett et al., 2012). In contrast, *V. dubyana* can survive intermittent desiccation events but is usually found submerged and rapidly loses water when exposed to dry air. This species may need to invest photosynthetically assimilated carbon to synthesize VTs to cope with the higher desiccation pressure and higher stress levels. These larger investments in photoprotection and carbon pools are most probably driven by the need to stabilize proteins and membranes and to remodel cell walls. Alternatively, it can be hypothesized that changes in VT profiles in bryophytes under desiccation may be related to a completely different function than direct stress protection. In fact, VOCs may have a communicating function in plants (Rosenkranz et al., 2021), even though VOC receptors have not been characterized in plants yet (Loreto & D'Auria 2022). Changes in VT profiles under desiccation may be interpreted as a release of warning cues for naïve (unstressed) bryophytes to induce biochemical acclimation to desiccation (Vicherová et al., 2020), or defences against biotic stress.

5 | CONCLUSIONS

The exploration of bryophytes' VT we collected data revealed several new key findings:

(1) distinctive VT profiles characterized species under optimum hydration conditions; (2) the VT pool at fully hydrated conditions decreased as desiccation tolerance increased; (3) while VT levels increased during bryophyte desiccation, there was a negative correlation with tolerance; (4) camphene was the only VT that increased significantly in the more DT species. Further investigation is necessary to investigate the variability in VT composition we observed among the bryophytes' species, which could be attributed to a complex interplay between ecological attributes, life form characteristics, and environmental factors.

AUTHOR CONTRIBUTIONS

Research conception and design were by RE, JIGP, FB, and FL, methodology implementation by RE, SP, FB, and MM, experiment execution and data collection by RE, SP, FB, and MM, data analysis/interpretation by RE, SP, FB, JIGP, IO, MM, and FR, data discussion and manuscript draft writing by RE, SP, FB, GPJI, MM, and FL, and final writing and revision by all authors.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article in the absolute amount of individual VTs (ng g^{-1} DW) in the bryophyte species: *P. squarrosa*, *P. platyphylla* and *V. dubyana*.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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