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An insight into drought resilience in three cohabiting mosses

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Drought stress is one of the critical abiotic stresses and it severely affects plant growth and development. Mosses, have an ability to pass in and out of physiological inactivity (anabiosis), which makes them a suitable plant group for drought stress studies. In this study, we investigated the differences in drought resistance among three phylogenetically distant but cohabiting moss species, namely *Pleurozium schreberi*, *Polytrichum formosum* and *Rhytidiadelphus squarrosus* under simulation of drought caused by PEG600, as inferred by the ion leakage, relative water content (RWC) and membrane stability as inferred by lipid peroxidation status. These parameters enable the understanding of the drought stress tolerance capacity and to determine drought resilience of the three selected moss species. *Polytrichum formosum* seems to tolerate the drought stress better than the other two mosses. It is also statistically supported that its membranes are less damaged, compared to other two tested species.

Keywords: Bryophyte, Ion leakage, MDA, RWC, Stress, Water lack

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INTRODUCTION

Plants suffer from rapid and extreme changes in their environment caused both by biotic and abiotic factors. One of the main stress factors to all living beings is drought or water scarcity, and for sessile organisms like plants, drought, i.e. water deficiency can be lethal. Climatic changes with severe fluctuation and extended drought period directly influence the survival of many plant species. Among them, the bryophytes without developed root systems and cuticle seem to be more sensitive and are affected by the drought. However, in such a diverse group of land plants, they evolved in many directions and find ways to cope with different environmental challenges including drought. The most spectacular one is to enter the anabiosis state and to resurrect rapidly in a short period of optimal condition (Cushman & Oliver, 2011). There are many other indistinct mechanisms applied to survive in a harsh environment. Apart from anabiosis, the drought tolerance and resistance mechanisms are not evenly distributed among bryophyte representatives. There are probably many possibilities to cope with stressors in different species.

Bryophytes can grow and adapt to any natural habitats; i.e. terrestrial, freshwater, or to any extremely harsh environmental conditions even those having no life necessities for other plants. They are absent from the sea water ecosystems although there are specialists that can live in brackish water or cope the high level of salt in the substrate (Ćosić et al., 2019).

Many bryophytes fall under the category of poikilohydric plants which mean that moss body hydration is fully equilibrated with level of water present in environment (Šinžar-Sekulić et al., 2005). This remarkable feature allows the moss to pause for a while and recommence all the physiological processes related with the water as per the fluctuations in their availability (Zhang et al., 2021). The complete absence of water, i.e. drought conditions of substrate, absence of precipitates or insufficiency of the relative content of water vapor in the atmosphere has a negative impact on plant growth and metabolism of bryophytes. Unlike vascular plants, mosses take up and depend on water availability from the environment, i.e. their water balance is equilibrated to the water balance of the surrounding area. Several moss species found in dry and moderate water scarcity conditions have been subjected to the study drought stress, which gives us more insights about the adaptive mechanisms in this group of plants (Seel et al., 1992; Widiez et al., 2014), i.e. different gene activation during the juvenile to adult transitions or the variation in the intensity of physiological processes like respiration and photosynthesis decrease and significant changes in biochemical parameters under single or combined stresses. Cong et al. (2021) also highlighted the need for more studies of such types bearing in mind, that many mechanisms and processes in bryophytes during drought stress remain obscured and are insufficiently known.

Here, we studied the resilience of the three selected cohabiting moss species, collected from the same site, at the same time, in close proximity to one another. The resilience was tested by drought simulation in mosses with polyethylene-glycol 600 causing water loss, and ion leakage from cells was measured for membrane stability. These moss species were selected according to their tenacity during the drought period in semi-open acidic grassland heat with scattered spruce tree, a montane habitat type of central Europe. The species selection was done in order to choose different life forms, various life strategies and phylogenetically unrelated taxa. Thus, two pleurocarpous mosses (prostrate *Pleurozium schreberi* (Brid.) Mitt., fam. Hylocomiaceae, mat forming *Rhytidiadelphus squarrosus* (Hedw.) Warst., fam. Hylocomiaceae) and one acrocarpous moss (*Polytrichum formosum* (Hedw.) G.L. Smith, fam. Polytrichaceae) were the subjects of this study.

Here, we aimed to find out the response(s) of few selected moss species, i.e. *Polytrichum formosum*, *Pleurozium schreberi* and *Rhytidiadelphus squarrosus* collected from the same microhabitats (growing within a square meter) and if there is a difference in adaptive mechanisms to drought even if they grow together at the same spot.

MATERIALS AND METHODS

Study area

The samples were collected from Kojšovska Hol'a Mt. in the district of Gelnica in eastern Slovakia (leg./det. Michal Goga and Marko Sabovljević, on 19th October 2022, open grassland on the hill heats, 48° 46' 52.0062" N, 20° 58' 45.7644" E, 1240m a.s.l.). The day, when moss was collected, was cool (+4ºC), cloudy and windy. The general climate type of the sampling site is montane, mild-continental one, with cool winters, hot summers and drought during the summer period.

Material

Three mosses were selected at the same spot growing together in the semi-shade condition of the open grassland near the stunted spruce tree (*Picea abies* (L.) H. Karst.) based on anatomical, morphological, life form and strategy distinctiveness (ectohydry vs. endohydry or pleurocarpous vs acrocarpous), namely *Pleurozium schreberi, Polytrichum formosum* and *Rhytidiadelphus squarrosus*.

Rhytidiadelphus squarrosus (cushion) and *Polytrichum formosum* (tuft) grow on soils which are strongly acidic to nearly neutral, but most frequently/ regularly in mildly acidic conditions. Also, it occurs in upland woodlands on leached soils and well-drained moorlands. It can be found on lowland heaths, avoiding the wettest areas. *Pleurozium schreberi* (weft) avoids calcareous or base-rich habitats, and is most commonly found amongst grass and heather on heathland and in open, healthy woods. In such places, it can be truly abundant. All above mentioned species are mesophytes, semi-sciophyte and inhabit moderately infertile sites.

Sample preparation

After collection, samples were manually cleaned to a prevent the unwanted materials from nature, and were stored in sealed plastic bags at 4ºC for a short term (24h) till the experimentation was carried out. The short but adequate storage was crucial for measuring the relative water content. Therefore, the material were brought to the laboratory within 24h in a portable refrigerator at (+4ºC). Only green parts and tips of the mosses were used to avoid artefacts by measuring or threatened by old, less functional and dead parts of mosses.

Experimental design

The young moss apical shoots (10mm long) were weighted (300mg) and further analysed. The weighted mass was divided into two series and kept for 24 h hydration at room temperature (22°C) by rinsing them into distilled water. The first series was used to further measure and calculate the relative water content for each species.

The second series was treated with polyethylene-glycol 600 solution at a concentration of 232g/L for another 24h and control samples were treated with 10ml of double distilled water prior to measurement of the ion leakage by the solution conductivity. Malondialdehyde content was also measured in the similar manner. The specific PEG600 concentration was selected to achieve 1.67 MPa in order to induce drought stress in mosses and tracheophytes as described previously by Šinžar-Sekulić et al. (2005). Further, the moss plants (treated and controlled) were transferred to double distilled water and quantity of ion leakage (solution conductivity) was measured in hourly intervals. After the completion of this measurement 100mg moss samples were weighed (both treated and controlled) and were kept in plastic bags, and stored at -80°C for further malondialdehyde (MDA) analysis. Each experiment was performed in three replicates.

Through this analysis, oxidative stress and lipid peroxidation were determined, as a consequence of induced desiccation stress.

Relative water content (RWC)

Measurement of RWC is one of the prime methods to observe the water holding capacity of plants for the water available in the environment they are found, as the RWC gradually declines with the increase the drought conditions (Proctor et al., 1998; Farooq et al., 2009).

Relative water content (RWC) was determined by following formula:

$$RWC(\%) = [(FW - DW) / (TW - DW)]*100$$

where: FW is weight of plants in fresh state, and DW the weight of totally dried out plants to/of constant weight, and TW is fully hydrated weight of plants.

All three moss species (300mg) were taken for RWC assay. The FW was measured soon after the moss plants were collected from nature. The full turgid weight (TW) was determined after soaking the moss samples in water for 24h. The dry weight (DW) was obtained after keeping the moss plants for 48h at 80°C in an oven until it reached the constant weight.

Ionic conductivity assay

Measurement of conductivity proves to be useful to understand the stress tolerance levels among bryophyte and acts as a suitable indicator of membrane damage (Cruz de Carvalho et al., 2017). For the experiment, young apical shoots of moss plants with a length of approx. 10mm were considered. Moss plants (300mg) were added to the test tubes with 10ml of PEG600 at a concentration of 232g/L and 10ml of distilled water for the treatments and control conditions respectively. The samples were left in this condition for 24h at room temperature. After the given time, the moss plants were transferred into test tubes filled with deionized water with a volume of 10ml. With the help of a conduct meter using a SI Analytics Lab955, ion conductivity was measured at different times (1h, 3h, 5h, 7h, 9h) intervals.

Malondialdehyde (MDA) assay

All the three moss plants were fully hydrated before subjecting them to simulation of the drought stress for respective hours along with the control samples, and immediately transferring them to -80°C for further MDA measurements. The level of lipid peroxidation in plant tissue was determined as 2-Thiobarbituric acid (TBA) reactive metabolites chiefly malondialdehyde (MDA) as described previously (Heath & Packer, 1968).

Moss plant material (100mg) was extracted in 2ml of 0.25% TBA made in 10% TCA (trichloroacetic acid). Later the extract was heated at 95℃ for 30min and then quickly cooled on ice which results /resulted into precipitation of the proteins. After centrifugation at 10,000rpm for 10min, the absorbance of the supernatant was measured at 532nm. The level of lipid peroxidation was expressed as micromole of MDA content formed using an extinction coefficient of $155mM^{-1}cm^{-1}$.

Lipid peroxidation is a sequential reaction that produces a steady supply of free radicals, causing additional peroxidation and the accumulation of free radicals, resulting in oxidative stress (Liu et al., 2013).

Statistical analysis

The statistical analysis was conducted using R programming language (v. 4.3.1) (R Core Team, 2022). Different types of analyses were carried out depending on the data obtained. In case of relative water content data, a non-parametric Kruskal-Wallis test was used for group comparisons, followed by Dunn's post-hoc test for multiple comparisons with Benjamini-Hochberg p-value adjustment method. The significance level (α) was set at 0.05.

For conductivity and MDA content data, a non-parametric factorial ANOVA was performed using the Aligned Rank Transform (ART) method (Wobbrock et al., 2011; Elkin et al., 2021). Factorial models were created using the "art" function from the "ARTool" R package (Kay et al., 2021), and the significance of main effects and interactions was evaluated using the "anova" function. Contrast tests were carried out using the "art.con" function from the same R package.

RESULTS

The results obtained clearly shows that there are differences in drought resiliencies among the three tested mosses.

A rather high relative water content (RWC) of 60.5% was observed in *Polytrichum formosum,* followed by 56.5% in *P. schreberi*. The Smallest inner water ammount (RWC of 37.5%) was documented in *Rhytidiadelphus squarrosus* (Figure 1). The obtained values depict the relative situation as it is in the field under condition of non-high radiation, on cool but windy autumn day.

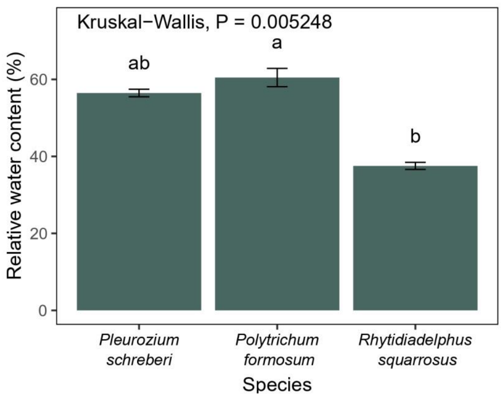

Figure 1. Relative water content of *Pleurozium schreberi, Polytrichum formosum* and *Rhytidiadelphus squarrosus* [Data are presented as mean ± standard error. Different letters above the bars indicate statistically significant differences (P< 0.05) between the tested species]

In *Pleurozium schreberi* and *Rhytidiadelphus squarrosus*, the main effects of PEG treatment and exposure time, along with their interaction, significantly influenced both ion leakage as inferred by surrounding water solution conductivity measures and, MDA content (P < 0.01) (Table 1 and Figure 2). The analysis showed highly significant effects of PEG600 treatment on both parameters (P < 0.001), confirming the effects of drought in two tested species.

In case of *Polytrichum formosum*, the results varied. While both treatment and exposure time had significant effects on conductivity i.e. ion leakage from the moss cytoplasm to water solution (P < 0.001), the main effect of PEG600 treatment on MDA was not statistically significant (Table 1). However, statistically, treatment duration itself and the interaction between treatment duration and PEG effect significantly influenced MDA (P< 0.01).

The damage of the moss cell membranes by PEG600 varies in different time intervals. The control plants kept in distilled water also show some cell membrane damage by the increase of conductivity but it is rather less compared to plants treated with PEG600. The differences among values of initial hour of treatments varied among 15.47µS/cm and 18.73µS/cm and in control among 12.49µS/cm and 16.9µS/cm in both *P. formosum* and *R. squarrosus,* respectively. There is negligible difference in the values of treatment and control i.e. 10.3µS/cm and 10.4µS/cm respectively in *P. schreberi*, suggesting this species to be rather resilient to short-term water shortage.

Interesting values were obtained 9h after the beginning of treatment with PEG600, since the conductivity in all treatments increase significantly compared to controlled plants due to higher membrane damages and ion leakage to the water solution. In all three moss species maximum values were documented and thus for *R. squarrosus* 22.43µS/cm, *P. formosum* 22.23µS/cm and least for *P. schreberi* 14.06 µS/cm. This can be a marker to infer that *P. schreberi* possesses some mechanisms of keeping its cell membranes relatively stable under short drought stress condition and thus to be less prone to drought stress.

The results show the increase of the induced drought stress level with time duration among all three moss species as inferred by the MDA values. The values of 9th hour after the application of PEG600 to the treated moss plant, showed to be the highest in *R. squarrosus* (0.079497155μM g^{-1} DW) which is comparatively lower in *P. schreberi* (0.064551021μM g^{-1} DW) and the lowest in *P. formosum* (0.013175888μM g^{-1} DW). The values for the same moss species in controlled condition (water free of PEG600) are rather lower. In *R. squarrosus,* it is 0.0763μM g^{-1} DW, while in *P. formosum* it is 0.0165μM g^{-1} DW which is negligible compared to the treatment 9h after application of PEG600. When compared with treatment the values from the controlled condition are significantly higher in *P. schreberi* 0.0919μM g^{-1} DW.

Table 1. Summary results of the factorial analysis, evaluating the effects of PEG600 treatment, Time, and their interaction (Treatment × Time) on the conductivity and MDA content in *Pleurozium schreberi*, *Polytrichum formosum* and *Rhytidiadelphus squarrosus*.

Species	Parameter	Treatment PEG600	Time (duration)	Treatment × Time
Pleurozium schreberi	Conductivity	85.7359***	24.2463***	4.1085**
	MDA	54.6098***	4.6344**	7.4272***
Polytrichum formosum	Conductivity	12.6738***	16.1060***	1.2546
	MDA	3.6787	4.8906**	5.3461**
Rhytidiadelphus squarrosus	Conductivity	23.9667***	6.2204***	4.8057**
	MDA	71.812***	12.286***	17.902***

The values represent F values, with the asterisks indicating the corresponding level of statistical significance, ** $P < 0.01$, *** $P < 0.001$

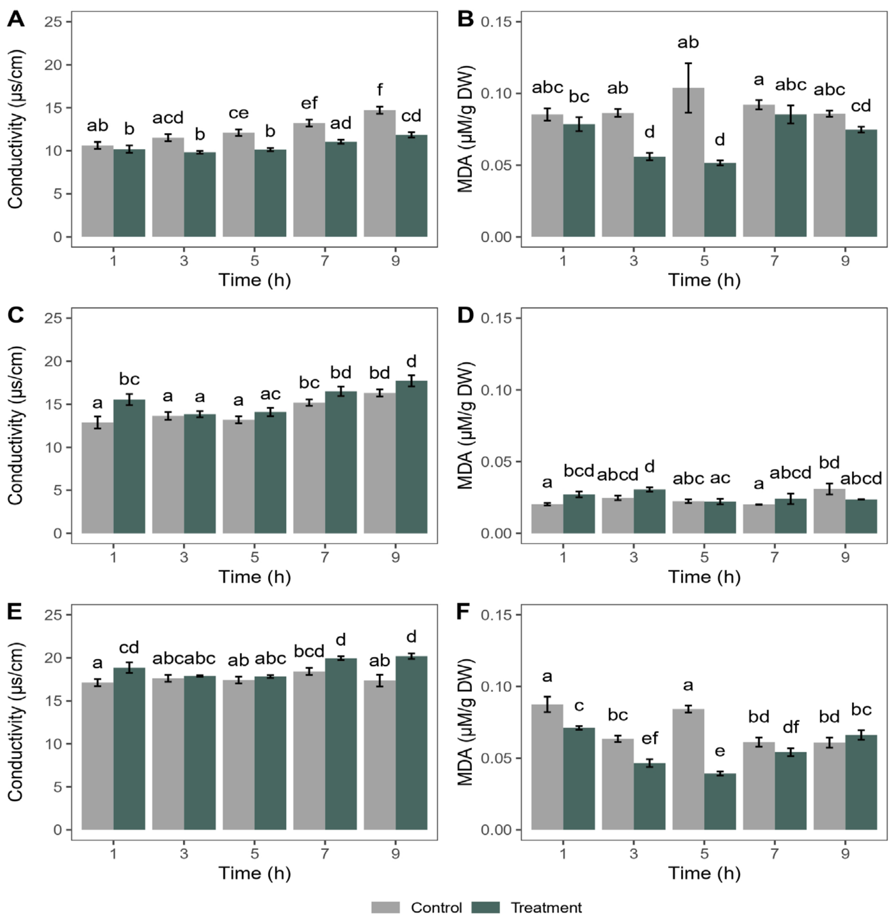

Figure 2. The effects of 232g/L of polyethylene glycol (PEG600) and different exposure times on ion leakage, i.e. conductivity of solution and malondialdehyde (MDA) in *Pleurozium schreberi* (A, B), *Polytrichum formosum* (C, D) and *Rhytidiadelphus squarrosus* (E, F) [Data are presented as mean ± standard error. Different letters above the bars indicate statistically significant differences ($P < 0.05$) between the experimental groups]

DISCUSSION

The results clearly showed that the species are resilient to induced drought stress to some extent and that the strategies and mechanisms to tolerate and to resist drought stress are different. According to the data obtained, *Polytrichum fomosum* seems to be rather resistant to short term drought stress, since all the parameters indicated any damages caused by induced drought stress and obtained in this study were significantly lower compared to other two species. This species belongs to the Polytrichales, a group of mosses where the appearance of primitive conductive vessels was evolutionary forerunner to tracheophyte. Additionally, this species has other morpho-anatomical adaptation as well as photosystem protection and recovery mechanisms to drought and high light radiation survival (Proctor et al., 2007). Here, we additionally document the ability of this species to survive harsh environmental condition, by maintaining cell membrane stability (in comparison to two other tested species). Additionally, endohydry (inner conductivity of water) is documented for this species, which means it resembles somewhat to vascular plants by absorbing and transporting water internally through a well-developed conducting strand (namely vessels of hydrom) and it is assumed that this is also supported through basal rhizoidal system (Polytrichaceae and some thallose liverworts) as stated by Proctor (1982). This resulted in a slower process of achieving full turgidity in such species, but also in slower water loss. In contrast, predominantly ectohydric species absorb and move water primarily across their surface via capillary action (e.g., leafy liverworts and the most mosses), allowing them to become hydrated rather quickly (Proctor, 1982), but also to loose water rapidly.

Apart from *P. formosum*, the other two tested species showed similar values and patterns of MDA during drought stress simulation, inferring allied lipid peroxidation level under drought stress. Though, in *P. schreberi* ion leakage from the cytoplasm is slightly lower indicating better tolerance of water shortage, at least for the short period as compared to *R. squarrosus*.

Indeed, bryophytes have also adapted to very dry zones of the earth surface. Being poikilohydric in nature, they are always benefitted in maintaining a counter balance with the moisture present in their surroundings (Tuba et al., 1996).

Among this group of plants some moss species are tolerant to short period of dryness whereas others can survive longer durations and can maintain the capacity to function well after the return of favorable conditions. These facts can also influence the species spread and its micro-habitat overlapping within the same distribution range. Apart from eco-physiological properties, the life forms and strategies as well as evolutionary history are significant factors in species composition and interaction. *Polytrichum formosum,* as well as other species from the genus, forms rather dense patches with upright shoots as an adaptation to reduced water loss (Longton, 1970, 1979). There is no strong air flow around each patch , which means less water vapour is flowing away from the moss plant resulting to slower moss desiccation. Like many other mosses, they tightly appress their leaves to the stem to minimize water loss (like other two studied species as well), but *P. formosum* additionally has curved and twisted leaves in order to decrease its outer surface to protect the numerous lamellae it has above the costa part, significantly during wet season.

Consequently, water content also differs between species, reflecting their habitat preferences but also structural characteristics, as shown also in present study (Rundel & Lange, 1980).

The hydration status is regulated by many elements, including air temperature, relative humidity, vapor deficit, air pressure, radiation, and wind speed in their environments, along with plant phenology and water consumption efficiency (Elumeeva et al., 2011; Zhang et al., 2016). The variation of RWC among bryophyte species ranging from 36% to 416% of dry weight, and this can significantly change with small variation of one environmental factor (e.g. sun radiation intensity) as stated by Köhler et al. (2007) and Coelho et al. (2023). In our comparative study of three moss species which were collected on the same day at a same site (during cloudy, chilly and windy day), RWC (depicting level of moss body hydration) still varying between 35% and 60% among them. The values showed that the hydration status of tested plants was rather low and significantly different among some of them, allowing better comparison.

The pleurocarpous moss *P. schreberi* exhibits similar ion leakage patterns to those observed in *P. formosum*. However, despite these similarities, the two species not phylogenetically related, have distinct life forms, and possibly employ different strategies to cope with drought stress. The slightly lower ion leakage values in *P. schreberi* suggest that it may possess somewhat better drought tolerance. Though, *P. formosum* contains leptoids and hydroids as conductive vessels, but the water conduction in this species remains primarily external, and it is erect and larger in size, as well as life form inferred to that this species generally better support short-term drought.

The third species tested, *R. squarrosus*, appears to be the most sensitive to rapid drought stress, as indicated by its high ion leakage values. However, it is important to note that these values remain within the smallest range among the three species tested, suggesting relatively good membrane stability during the measurement period. After the initial drought stress shock, the membrane stability in *R. squarrosus* remains consistent, with no additional damage observed. The changes in the relative membrane permeability of the other moss species namely *Didymodon fallax* (Hedw.) R.H. Zander, *Erythrodontium julaceum* (Schwaegr.) Par. and *Bryum argenteum* Hedw., also shows the similar patterns like the selected moss species in our study (Zhang et al., 2017).

Plants, including mosses, possess an antioxidant system that detoxifies excess reactive oxygen species (ROS) at least at the beginning of the stress conditions through both enzymatic (catalase (CAT), super-oxide dismutase (SOD) and guaiacol per-oxidase (POD)) and non-enzymatic antioxidants (glutathione (GSH), vitamin C, and carotenoids). (Zhang et al., 2017). Stress has frequently been shown to enhance the activity of these enzymes. For example, in the drought-tolerant moss species *Syntrichia ruralis* (Hedw.) F. Weber & D. Mohr, the activities of SOD and catalase reached their peak levels after 5 hours of slow drying (Dhindsa & Matowe, 1981). For example, SOD activity was greatly increased during desiccation in the moss *Atrichum androgynum* (Müll. Hal.) A. Jaeger (Mayaba & Beckett, 2003), while *Dicranum scoparium* (Hedw.) Sm. has shown maximum presence of POD while exposed to slow drying conditions (Onele et al., 2018), for the short term. Increased production of reactive oxygen species (ROS) can lead to lipid peroxidation, compromising membrane integrity and increasing its permeability. As a result, the relative permeability of the plasma membrane serves as an indicator of the extent of damage to the cell structure (Cruz de Carvalho, 2008).

The studies on desiccation tolerance in one of the empirically less tolerant moss species *Dicranella palustris* (Dicks.) Crundw. ex E.F.Warb. have shown the increased concentration of MDA in comparison with the other tolerant moss species *Syntrichia ruraliformis* (Besch.) Cardot (Seel et al., 1992; Ruchika et al., 2021). Similarly, in our study, documented MDA level is higher in moss *P. formosum*, comparing with the other two moss species. Malondialdehyde, when expressed per dry weight, was rather higher in treatments but only for a short period suggesting that lipid oxidation appears at the very beginning of drought stress.

The MDA analyses in the moss *P. schreberi* did not show us any clear pattern or trend of membrane lipid oxidation after 24h drought stress period. The results obtained clearly show the differences between treatments and control plant groups but not the trends that can be directly related to drought stress simulation. However, it is obvious that this species within the treatments are rather non-responsive to membrane lipid oxidation compared to control moss groups, which suggests a rather high resistance of this species to drought stress.

CONCLUSION

This comparative study may influence the similar research which is based to focus on the potential moss species tolerant to drought stress. The results obtained here suggest that the degree of tolerance to drought stress varies with respect to the duration and intensity of stress experienced by the tested moss species. Among the three moss species considered for our study, both, ion leakage and MDA analyses clearly showed that *P. schreberi* is well adapted to short term drought stress, while *P. formosum* and *R. squarrosus* have different strategies in survival of drought stress, i.e. it reacts rapidly to drought stress. However, *P. formosum* seems to be the most drought tolerant and resiliant to wáter shortage, at least for the transient period. This gives deeper insights and furthermore, better understanding of the adaptive mechanisms and strategies implemented by mosses growing in the similar environmental conditions for the stress tolerance towards drought. The data from this study holds significant ecological value, especially bearing to mind severe climate changes, unevenly spread of precipitates and longer period of water shortage and their survival.

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Declaration: The authors declare no conflict of interests.

Authors' contributions: MB, MSS, and MG designed the study, conducted the experiments, collected the samples, and revised and edited the manuscript. PS, DPB, and DR carried out the experiments, performed the formal analyses and statistical evaluations, and drafted the manuscript.

Ethical approval: Not applicable.

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