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ARTICLE

Photosynthetic responses of the desiccation intolerant *Sphagnum angustifolium* in relation to increasing its desiccation tolerance by exogenous ABA

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ABSTRACT Photosynthetic responses were used to study the effect of exogenous ABA on aspects of desiccation tolerance in a desiccation intolerant bryophyte, *Sphagnum angustifolium.* CO_2-fixation in *S. angustifolium* and higher plant cells responded similarly to water deficit caused by natural or controlled drying. Ch fluorescence parameters were monitored during slow or rapid desiccation and also upon rehydration. Fv/Fm and ΦPSII were generally higher in ABA-hardened plants under intensive water stress (below 50% of RWC). ABA-hardening improved recovery of PSII activity upon rehydration, and it resulted in an effective protection of PSII activity against light stress. Activity of PSI was less influenced by exogenous ABA. In the course of slow drying increased thermal energy dissipation was detected. NPQ in *S. angustifolium* – not like in DT bryophytes- saturated with increasing irradiance. During desiccation NPQ did not change until 50% of RWC in ABA-hardened plants, while it increased in control plants. Unlike *Atrichum*, increased desiccation tolerance was not accompanied by increased NPQ and decreased PS2 efficiency.

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KEY WORDS

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Desiccation tolerance is general in the poikilohydric bryophytes, but not universal. Cell water relations in bryophytes essentially are the same as those of other plant cells. Different adaptive types of bryophytes and higher plant cells respond similarly to water deficit. Therefore bryophytes are ideal model plants to study the physiological basis of desiccation tolerance.

The inducible mechanisms of desiccation tolerance were investigated in the desiccation sensitive *Sphagnum angustifolium*. This plant lives in a constantly wet habitat and it also has a very effective water holding morphology to avoid desiccation (Hájek and Beckett 2008). If its chlorophyllose cells lose their turgor and they do not get any water supply from their surroundings, they dry quickly and lose their photosynthetic activity. *S. angustifolium* is a typical hollow forming species. Hummock forming *Sphagna* are exposed a lot better to drought, than the hollow forming ones, therefore they have relatively larger water holding capacity, than the hollow forming species have (Hájek and Beckett 2008). Due to their wet habitat preference and their morphological adaptation *Sphagna* successfully avoid desiccation. Their strategy is like a „drought avoidance" strategy in vascular plants.

Genes required for desiccation tolerance appear to be present in most if not all plants, as indicated by molecular studies (Bartels and Salamini 2001). So the genetic potential for desiccation tolerance may be universal, which means it is also present in desiccation intolerant species, but genes associated with tolerance often are not expressed. Desiccation tolerance can be induced gradually by acclimatization in sensitive species in certain limits.

Our data focus on the photosynthetic responses, photoprotective mechanisms of *S. angustifolium* during desiccation and upon rehydration after ABA-hardening.

Materials and Methods

S. angustifolium originated from north-east Hungary and were acclimatised at 100% RH in desiccators at 16°C, at a PPFD of 100 μmol m^{-2} s^{-1}, and a photoperiod of 12/12 light/dark for 1 month before treatments.

Measurements of water status dependence on P_n were carried out at 16°C, at a PPFD of 600 μmol m^{-2} s^{-1} on samples with known RWC. These experiments started at full turgor of the plants (~1400% RWC dw), followed by 'natural drying' (at 16°C, at a PPFD of 100 μmol m^{-2} s^{-1} and 35% RH), or controlled drying (in desiccators at 54% RH and at 16°C, at a PPFD of 100 μmol m^{-2} s^{-1}) or controlled levels of osmotic stress by exposure to PEG (4000) solutions.

Plants were pre-treated with 0.1 mM ABA or distilled water (control) for 1 h and stored hydrated for 12 or 36 hours before measurements at 20°C and a light intensity of 45 μmol PAR $m^{-2}s^{-1}$ under continuous light. It was followed by intensive rapid drying (in desiccators over silicagel), or slow

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gradual drying (in desiccators over sat. calcium-nitrate) After rehydration CO_2-fixation, and chl fluorescence parameters were monitored from 1 hour to 216 hours.

In vivo chl fluorescence was measured using a Dual-PAM-100 chl fluorescence & P700 photosynthesis analyzer. The changes in chl fluorescence intensity, and the activity of PSI were determined simultaneously. The experimental protocol, terminology and calculations followed Van Kooten and Snel (1990), and Klughammer and Schreiber 2008 for measuring P700. CO_2 assimilation was measured in normal air by IRGA in an open gas-exchange system using a T controlled leaf chamber. Assimilation rates (*A*) were calculated after von Caemmerer and Farquhar (1981).

Results

In the course of 'natural drying' the photosynthetic activity (P_n) of *S. angustifolium* falled to 0 in 90 mins, while RWC (as % dw) decreased to ~25% from full turgor. *A* was stable until RWC = 0.4 (as % of WC at full turgor) and then continued to decrease almost linearly to 0.1. Applying controlled drying at RH 54% *A* declined slowly and after 5 h-desiccation it reached ~40% of its value at full turgor. -0.2481 MPa osmotic stress resulted in 9% decrease in *A* after 1.5 h and 50% after 24 h exposure.

Photosynthetic activity in *S. angustifolium* and higher plant cells responded similarly to water deficit. Photosynthetic responses of various plant species (bryophytes and higher plants) having different photosynthetic and desiccation tolerance adaptation strategy were similar under various levels of water stress if effective water status of bryophytes was correctly determined.

Electron transport rate (ETR) of PSII above 200 µE PPFD in ABA-hardened *S. angustifolium* was significantly higher, than in control plants. ETR of PSI was not affected by exogenous ABA. The mechanisms activating upon ABA-hardening may be protect the operation of PSII against of light stress as well. The activity of PSI is less sensitive to water stress and light stress, and it can hardly be affected by ABA which has a central role in osmotic signalization. In ABA-hardened plants NPQ values were lower with the increasing PPFD than in control plants (not like in *Atrichum*, as it was shown by Beckett et al. 2005, and Marschall and Beckett 2005). This probably means that ABA-hardening at full turgor activated a protective mechanism system, which induced photoprotective mechanisms in PSII, and at higher light intensities plants were not needed to dissipate the whole extra excitation energy as heat. The value of *1-qP* indicated lower light stress symptom in ABA-hardened plants compared to control plants. During intensive desiccation in both ABA-hardened and control samples maximal quantum yield (Fv/Fm) of PSII decreased to 80%, effective quantum yield (ΦPSII) of PSII to 50% at 50% of RWC. Average values of Fv/Fm and ΦPSII were generally higher in ABA-hardened plants under intensive water stress (below 50% of RWC). Upon rehydration Fv/Fm and ΦPSII significantly differed to the values of control plants. 24 hours after rehydration the recovery of Fv/Fm was 54% in ABA-hardened plants, while it was only 7% in control plants. During the course of rehydration ΦPSII was constant both in ABA-hardened and control plants, but values in ABA-hardened samples were always higher. 216 hours after rehydration ΦPSII recovered in 45% in ABA-hardened plants, and only in 12% in control plants. During desiccation NPQ did not change until 50% of RWC in ABA-hardened plants, while it increased in control plants. Below 50% of RWC NPQ started to decrease in both samples, but the decrease was more intensive in control plants. 9 days after rehydration NPQ recovered in 80% in ABA-hardened plants, while recovery of the parameter was not detected in untreated plants. *qP* was similarly low in both types of samples during rehydration. In the course of slow drying in *S. angustifolium* an increased thermal energy dissipation was detected. This phenomenon is known for DT bryophytes (Proctor and Smirnoff 2011). During slow desiccation of *S. angustifolium* variable fluorescence ($\Delta F = F_m - F_0$) was lost and F_0 fluorescence was quenched. NPQ in *S. angustifolium* – not like in DT bryophytes- saturated with increasing irradiance.

Discussion

Photosynthetic activity in *S. angustifolium* and higher plant cells responded similarly to water deficit. ABA-hardening resulted in an effective protection of PSII activity against light stress. Exogenous ABA maybe shifts the photosynthetic apparatus from a "high efficiency" state to a less efficient but "photoprotected" state and upon rehydration it allows regeneration of photosynthesis starting from more favourable basis. Presumably exogenous ABA elicits the signal of osmotic stress in cells, which helps to induce an ABA-responsive signal transduction pathway to withstand stress condition. As in DT bryophytes is described, in the course of slow drying in *S. angustifolium* increased thermal energy dissipation was detected. The values of NPQ were lower in ABA-hardened plants, than in control plants and NPQ saturated with increasing irradiance. Activity of PS I was hardly influenced by exogenous ABA.

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