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Photosynthetic responses in the inducible mechanisms of desiccation tolerance of a liverwort and a moss

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ABSTRACT Chlorophyll fluorescence was used to study the effect of hardening treatments on aspects of desiccation tolerance in the liverwort *Dumortiera hirsuta* and the moss *Atrichum androgynum.* After desiccation the recovery of PS2 was monitored during rehydration. We show that partial dehydration and ABA treatments can increase desiccation tolerance. In *A. androgynum*, the increased desiccation tolerance is accompanied by increased NPQ. However, hardening decreases the efficiency of photosynthesis in unstressed plants as well. In *D. hirsuta*, as for *Atrichum*, treatment with ABA greatly increased desiccation tolerance. *D. hirsuta* was much more responsive to ABA hardening than *Atrichum*. Unlike *Atrichum*, increased desiccation tolerance was not accompanied by increased NPQ and decreased PS2 efficiency. While partial dehydration hardening had little effect on the liverwort before stress, hardened plants displayed a moderate (22%) but significant improvement in PS2 activity 1 h following rehydration. As for the ABA hardening treatments, improved recovery of PS2 activity was not accompanied by increased NPQ, and NPQ was actually lower in hardened plants. Partial dehydration can increase tolerance in *D. hirsuta*, however, the increases were less than those induced by ABA.
The mechanism of the hardening-induced increases in desiccation tolerance appear quite different in the two species.

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KEY WORDS

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Bryophytes survive desiccation not by any one simple adaptive feature, but by a complex interplay of many mechanisms, including the production of protective carbohydrates and proteins, and enzymic and non-enzymic antioxidants (Beckett et. al. 2005).

Oliver et al. (1998) divided desiccation tolerant plants into two types: those that survive if drying is slow enough to induce mechanisms that either protect the plants during desiccation or facilitate recovery during dehydration and, secondly, those that tolerate rapid drying. These two strategies may be termed "constitutive" or "inducible" respectively. Only very limited information is available on the distribution of these strategies in desiccation tolerant plants. The advantage of inducible systems is that, unlike constitutive mechanisms, they do not divert energy away from growth and reproductions. The disadvantage is that a sudden, severe drought may not allow time for the induction of tolerance and thus plants may not survive. We hypothesized that inducible tolerance mechanisms would be selected for in environments that are usually moist, and in which they only occasionally (and probably slowly) desiccated on a predictable seasonal basis. Therefore desiccation tolerance varies also on a predictable seasonal basis, being much higher in the dry winter months. We chose two model species for studying the inducible mechanisms of desiccation tolerance: the moss *Atrichum androgynum* and the liverwort *Dumortiera hirsuta* (Marchantiales). In these bryophytes desiccation tolerance can be induced in the laboratory by storing plants partially dehydrated for several days or by treating them with the hormone abscisic acid (ABA), which can replace the partial dehydration.

Materials and Methods

Dumortiera hirsuta and *Atrichum androgynum* (C. Müll.) A. Jaeger were collected from the understorey in the Doreen Clarke Nature Reserve, Hilton, KwaZulu-Natal Province, Republic of South Africa (24°39'S, 30°17'E). This nature reserve is a small pocket of Afromontane forest in the mist belt region of KwaZulu Natal. Once collected, material was stored on wet filter paper for up to 3 weeks at 15°C and a photosynthetic photon flux density (PPFD) of 45 μmol PAR $m^{-2}s^{-1}$ under continuous light.

Partial dehydration: plants were hardened by reducing the relative water content of the thallus disks (d=1cm) or apical stem segments to 0.5 (by storing plants over sat. KCl, or in a specimen bottle in a container at 100% RH) for 18 hours (sat. KCl) or 3 days (in the specimen bottle) at 15°C and a light intensity of 45 μmol PAR $m^{-2}s^{-1}$ under continuous light. ABA-hardening: abscisic acid (± cis-trans, Sigma) was dissolved in a drop of 1M NaOH, and the pH of the resulting solution adjusted to 5.6 with HCl. Plant were pretreated with 100 μmol ABA or distilled water for 1 h and stored hydrated for 2 or 3 days at 15°C and a light intensity of 45 μmol PAR $m^{-2}s^{-1}$ under continuous light. Hardened and non-hardened

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*Corresponding author. E-mail: marschal@ektf.hu plants were then desiccated for 16 h by placing the thallus disks or the stem segments in 2 x 5 cm specimen bottles in a desiccator over silica gel at 15°C and a light intensity of 45 μmol PAR $m^{-2}s^{-1}$ under continuous light, and then quickly rehydrated in the dark or in the light (100 μmol PAR $m^{-2}s^{-1}$) by adding deionized distilled water. Chlorophyll fluorescence parameters were measured before and after hardening, after desiccation and 1, 5, 9, 33 and 100 h after rehydration. Chlorophyll fluorescence was measured using modulated fluorometers (Hansatech, PAM-2000). To calculate fluorescence parameters we followed Schreiber and Bilger (1993) and Schreiber et al. (1995).

Results and Discussion

Studying inducible mechanisms of desiccation tolerance we found that various hardening treatments (partial dehydration and ABA) can increase desiccation tolerance in the liverwort *D. hirsuta* and in the moss, *A. androgynum*. In *A. androgynum*, hardening treatments do not increase desiccation tolerance by promoting the accumulation of sugar or by inducing free-radical scavenging enzymes (Mayaba et al. 2001). In *A. androgynum*, the mechanism for the increased desiccation tolerance seems to result from increased photoprotection by non-photochemical quenching (NPQ) and hardening treatments increased thylacoidal (qE) rather than reaction-based quenching (qI) during rehydration following desiccation. However, hardening also decreases the efficiency of photosynthesis in unstressed plants. Reduced PS2 efficiency could reduce net photosynthesis and, ultimately, the growth rate of the moss. Overall, our conclusion was that in *A. androgynum* hardening shifts the photosynthetic apparatus from a "high efficiency" state to a less efficient but "photoprotected" state. *D. hirsuta*, a very desiccation sensitive, shade-adapted species, can be a suitable object of study to obtain more information about the machinery of inducible mechanisms of desiccation tolerance. ETR saturates at a PPFD of 35 μmol photons $m^{-2}s^{-1}$ and light has a harmful effect on photochemistry over the range of a PPFD of 80 μmol photons $m^{-2}s^{-1}$. The disproportioning of the non-photochemical quenching parameters showed that the non-radiative energy dissipating mechanisms are responsible for 95% of the NPQ, while the slow relaxing (qI) 'photoinhibitory' component caused only 5% of the NPQ. In *D. hirsuta* we showed that, as in *Atrichum*, treatment with ABA greatly increased desiccation tolerance. We found that *D. hirsuta* was much more responsive to ABA hardening than *Atrichum*. Unlike in *Atrichum*, increased desiccation tolerance was not accompanied by increased NPQ and decreased PS2 efficiency. During rehydration in light after 3 hours ΦPS2 reaches the value of the unstressed plants in hardened material. While partial dehydration hardening had little effect on the liverwort before stress, hardened plants displayed a moderate (22%) but significant improvement in PS2 activity 1 h following rehydration. As for the ABA hardening treatments, improved recovery of PS2 activity was not accompanied by increased NPQ, and NPQ was actually lower in hardened plants. The data clearly show that partial dehydration can increase tolerance in *D. hirsuta*. However, the increases were less than those induced by ABA.

The mechanism of the hardening-induced increases in desiccation tolerance appear quite different in the two species.

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