

## Desiccation Tolerance: It's Mechanism

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### Introduction

Desiccation tolerance is an ancient and almost ubiquitous trait within land plants. In most, it is limited to their spores or seeds, but in a relatively small number of species, it is present in all vegetative tissues. Within the 383,671 known vascular plant species (80), only about 330(0.086%) are known to possess vegetative desiccation tolerance. The number of nonvascular plants that exhibit this trait is unknown because only a few of the estimated 20,240 species have been assessed. Wood reported that 210 (approximately 1%) bryophytes (158 mosses, 51 liverworts, and one hornwort) are desiccation tolerant, which is likely a significant underestimate given the plasticity of this trait in bryophytes (Oliver *et al.*, 2020). Vascular plants exhibiting vegetative desiccation tolerance are often termed resurrection plants because they seemingly revive from death when rewatered; this term is rarely used for nonvascular desiccation-tolerant plants. Desiccation tolerant organisms usually do not avoid water losses; instead, they deal with water removal by equipping themselves with protective molecules and by entering into a quiescent, metabolically inactive state (Alpert, 2005).

### Discovery of desiccation tolerance

The first observations of such a phenomenon were done by Antonie van Leeuwenhoek, a Dutch tradesman and scientist, who recorded them in his letter 'On certain Animalcules found in the sediment in gutters of the roofs of houses'. In this letter, he describes how certain 'animalcules' (today's microorganisms) would contract themselves into an oval shape when dehydrated and unfold their bodies upon re-watering to regain life (Keilin, 1959). He repeated these experiments many times with the same success and even 'animalcules' that were in a dry sediment that was kept in his study for months, were competent to regain life. Insightfully, van Leeuwenhoek also hypothesized that if such organisms could stay so long in a dry state and regain

life, this should be the way of survival in places where water bodies dry up during summer time or the dry season (e.g. in deserts).

### Role of desiccation tolerance in evolution of plants

Terrestrial organisms are constantly confronted with the desiccation stress imposed by air dryness. Consequently, during the evolution of plant life on land, adaptations that allow surviving and/or avoiding desiccation were required (Oliver *et al.*, 2005). The ability to tolerate near complete desiccation was an important evolutionary step that played a key role in dry land colonization. Likely, DT was primitively present in chlorophytic algae that were precursors of the basal land plants (Bryophytes, i.e. liverworts, mosses and hornworts) (Farrant and Moore, 2011). Bryophytes evolved mechanisms to limit water loss (cuticle and/or stomata) but the majority of bryophyte species are desiccation tolerant, which is an essential feature for life in habitats where water is not always available (Proctor *et al.*, 2007). Interestingly, genes responsible for synthesis and signalling of the dehydration stress hormone abscisic acid (ABA) are found in basal land plants and were likely important in the acquisition of DT and drought tolerance during plant evolution (Hauser *et al.*, 2011). In contrast to the Bryophytes, higher (vascular) plants rarely have desiccation-tolerant vegetative tissues. Currently, only some 330 resurrection plant species are known (0.15 % of the total number vascular plant species), which have been reported as desiccation tolerant in their vegetative parts (Proctor and Pence, 2002). In gymnosperms (e.g. conifers), DT is completely absent from vegetative tissues, which could be explained by the eco physiological constraint that excludes trees from being desiccation tolerant (Oliver *et al.*, 2000). Although DT is rare in vegetative organs of angiosperms, it is present in most seeds (~95 %) and pollen (~87 %) of the investigated spermatophyte species (Gaff and Oliver, 2013). Basal lineages of angiosperms do not contain any desiccation-tolerant plants (with DT in vegetative tissues), but they are found in later lineages,

suggesting that DT in vegetative tissues was lost early during plant evolution and regained later. In fact, DT re-evolved multiple times (at least 10) in the history of angiosperms, mostly within herbaceous lineages (Oliver *et al.*, 2000). It is hypothesized that in these plants the activation of already present DT mechanisms (from seeds and/or pollen) was the source of genetic reprogramming for DT acquisition rather than effective adaptation of abiotic stress responses (Farrant and Moore, 2011). In Spermatophytes, DT is mainly confined to seeds and pollen.

### Classification of plant on basis of desiccation tolerance

**1) Fully desiccation-tolerant plants:** Fully desiccation-tolerant plants are called so, because they can tolerate the total loss of free protoplasmic water (Oliver *et al.*, 1998) very rapidly. These plants rapidly equilibrate their internal water content with that of the environment because they possess very few morphological and physiological adaptations for water retention. The ability of rapid drying in this group of plants also strongly suggests that a constitutive protection mechanism is necessary for survival in this group of lower desiccation-tolerant plants (Oliver *et al.*, 2000). This sets the basis for the hypothesis that the primitive tolerance mechanism involves a constitutively protection mechanism coupled with active cellular repair (Oliver *et al.*, 2000). including the less complex clades that constitute the algae, lichens and mosses.

**(2) Modified desiccation-tolerant plants:** Modified desiccation-tolerant plants including most of the higher angiospermic resurrection plants. Modified desiccation-tolerant plants are more complex and relatively larger group of vegetative desiccation-tolerant plants. These plants usually dry slowly followed by a series of morphological and physiological mechanisms that reduce the rate of water loss to the extent required to establish tolerance. There are several evidences available for modified desiccation-tolerant plants which strongly suggest that they utilise preventive mechanisms that majorly rely on inducible cellular protection systems (Gaff, 1989).

### Changes observed during desiccation

**1) Morphological changes:** During dehydration in resurrection plants, morphological changes in

vegetative tissues occur to minimize the damage caused by excessive generation of free radicals. Among these, leaf curling or folding is the preliminary and the most obvious change observed. Leaves of *C. plantagineum* or *C. wilmsii* progressively curl inward during drying and become tightly folded so that only the abaxial surfaces of the older leaves in the outer whorl are exposed to the sun and become fully expanded upon rehydration (Sherwin and Farrant, 1998). These movements of the leaf along with the leaf folding are thought to reduce the transpiring surface and limit oxidative stress damage from UV radiation and are thus an important morphological adaptation.

**2) Lea proteins:** It is widely believed that protection during desiccation is afforded by the accumulation of various proteins, sugars and compatible solutes which serve to replace water and stabilize the sub-cellular environment by vitrification. Late embryogenesis abundant (LEA) proteins represent an important group of hydrophilic proteins which accumulate to high levels during the late states of embryogenesis in seeds when desiccation tolerance is acquired or in vegetative and reproductive tissues under dehydration suggesting a role in adaptation during desiccation. These proteins are predicted to have several protective functions which include protection of DNA, stabilization of cytoskeletal filaments and acting as molecular chaperones to protect protein conformation and activity. These are unable to protect the proteins from heat shock and they also cannot recover the activity of the proteins that are lost during dehydration process suggesting their role in the maintenance of protein activity and function during dehydration (Reyes *et al.*, 2005). It has also been shown that these proteins can act synergistically with sugars, such as trehalose to prevent protein aggregation during desiccation.

**3) Carbohydrates and desiccation tolerance:** In most cases, the ability of the plant to survive desiccation correlates with the accumulation of carbohydrates. If carbohydrates have a protective role, then they must be able to accumulate very rapidly and in sufficient quantity. So, the time required for the carbohydrate accumulation becomes a crucial parameter during dehydration. Accumulation of sucrose, trehalose as well as raffinose is commonly observed in dehydrating resurrection plants out of which trehalose occurs predominantly in desiccation-tolerant lower organisms including some vascular plants such as

*Selaginella tamariscina* and the moss, *T. ruralis*. Sucrose and raffinose are found in all angiosperms (Scott, 2000). In some of the resurrection plants sucrose accumulates as a product of photosynthesis. This conversion is directly correlated with an increase in the expression of sucrose synthase and sucrose phosphate synthase which result in the redirection of carbon flow from reserve substances such as starch or octulose to soluble saccharides such as sucrose. Thus, *Cratogeomys* has the capacity to accumulate sucrose very rapidly from carbohydrate sources already present in the leaf rather than relying upon photosynthesis.

**4) Small regulatory RNAs:** The significance of small RNAs in regulating plant responses to abiotic stress is now widely accepted. The application of exogenous ABA was able to induce desiccation tolerance in callus of *C. plantagineum*. Constitutive expression of CDT-1, a dehydration and ABA-inducible gene led to desiccation tolerance in callus and to the constitutive expression of dehydration and ABA responsive transcripts in *C. plantagineum* in the absence of ABA treatment. CDT-1 and other functionally related gene members have features of a short-interspersed element retrotransposon and are hypothesized to act as regulatory non-coding RNA molecules which are unique to *C. plantagineum*.

**Signaling mechanisms:** The general stress signal transduction in plants starts with the perception of the stress signal followed by the generation of secondary messengers which modulate the intracellular  $Ca^{2+}$  often initiating a protein phosphorylation cascade and finally targeting proteins involved in cellular protection or transcription factors controlling transcription of stress regulated genes. The products of these genes may participate in the generation of regulatory molecules like the phytohormone, abscisic acid (ABA).

Accumulation of ABA is one of the earliest responses observed in plants under drought stress. Apart from being a key player in the induction of desiccation tolerance, ABA regulates the expression of proteins such as LEA proteins (Hilbrich *et al.*, 2008). ABA has also been shown to be associated with the expression of several dehydration-regulated genes in resurrection plants. The information about genes that are involved in signaling and regulatory pathways in resurrection plants is limited in comparison to

*Arabidopsis*. In *C. plantagineum*, the synthesis of phospholipid-based signaling molecules is one of the earliest events in the perception of water stress. Two cDNA clones encoding phospholipase D have been isolated from *C. plantagineum* whose activity is induced by dehydration but not by ABA. The constitutively expressed CpPLD-1 transcript is thought to be involved in early responses to dehydration by producing second messenger molecules, whereas the dehydration-induced CpPLD-2 might be involved in phospholipid metabolism.

**Conclusion:** One of the most significant limitations upon crop productivity is the availability of water. During desiccation, different mechanisms of protection appear to act at different stages of water loss. During desiccation of plants and seeds, a complex array of structural, metabolic, chemical, mechanical and molecular changes occur to prevent potentially lethal cellular damage. Disruption of photosynthesis and respiration during desiccation and rehydration generates reactive oxygen species (ROS) that are the target of several protection mechanisms in tolerant cells. Metabolic responses to desiccation provide protection from both mechanical and chemical stresses (e.g., production of sugars that play an important role in cytoplasmic glass formation).

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