Minireview

What makes desiccation tolerable?

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Abstract

A comparison of drought tolerance in plants at extreme ends of the evolutionary spectrum is beginning to show the mechanisms involved.

It is no small feat for an organism, after losing more than 90% of its cellular water, to live and continue growing after rehydration. Many plants, one might argue, perform this trick when seeds develop; the topic here, however, is not seed maturation, dormancy and successful germination, but tolerance to extreme desiccation in the vegetative state. This involves, for example, the often rapid, non-destructive drying of existing leaves and their survival after water is returned. The ability to withstand such water loss is common to many algae and lichens, and is also found in liverworts, mosses, fern-like species and some ferns. The ability is missing entirely from gymnosperms but appears again in a few angiosperms. Oliver, Tuba and Mishler cover extremist strategies for survival under water deficit in a recent article [1] entitled 'The evolution of desiccation tolerance in land plants'. Their discussion offers an evolutionary view, outlines different strategies of tolerance acquisition, introduces emerging molecular genetic components, and finally outlines future work with a focus on genomic analyses. Knowing, it is argued, the genetic and biochemical makeup that brings about tolerance to vegetative desiccation might provide strategies to engineer protection of plants under less severe conditions.

When the precursors of higher plants first appeared on land - species without any water-conducting organs - desiccation stress became a possibility and a threat. Descendants of the early colonizers, the liverworts, hornworts and mosses (bryophytes), display implicitly primitive tolerance mechanisms by being 'always prepared'. They constitutively express proteins, which, while not totally protecting existing tissues

from damage during drying, minimize damage by a focus on the repair of cell structures during the rehydration phase. Repair capacity is stored in ribonucleoprotein particles (RNPs). Three foundations for survival are brought out by Oliver *et al*.: the first is to limit damage to existing tissues during desiccation so that repair is unnecessary or manageable (protection focus); maintaining life in the dried state is a second essential; and a third is mobilizing repair systems when water comes rushing back (restitution focus). The less complex species, bryophytes in particular, opt for the repair of damage to the cells upon rehydration, a strategy that comes with advantages and drawbacks. An advantage is that rapid desiccation can be tolerated; often the completely dried state may be reached in less than an hour. Yet even here a problem arises: tolerance to rapid water loss can only go so far, and variations exist among species. Increasing morphological complexity comes at the price of less tolerance or needing more time for additional preparations. Generally, the faster the rate of drying, the higher the potential for damage during desiccation and the less likely is survival, indicating that the theoretically constitutive nature of tolerance needs triggering, switches, and genetic and biochemical responses. The extremists have adapted to areas with unreliable rainfall, and to soils with minimal water retention. The main drawbacks seem to be low metabolic rates, possibly due to the cost associated with carrying the full 'survival gear' all the time, resulting in slow growth, and a limit to the size of plants for which this strategy can be made to work.

Repairing what has been damaged allows rapid water loss, whereas protecting what exists must be accompanied by much

slower drying. A dividing line can be drawn between the mosses and ferns: a line coinciding with the appearance of water-conducting structures, epidermal fortifications such as a waxy or reflective cuticle, thickening cell walls, or trichomes (hairs) curtailing the evaporation of water, and the emergence of additional anatomical, morphological and developmental complexity that accompanied the subsequent evolution of land plants and their adaptation to different habitats. Vegetative desiccation tolerance was eventually lost. It is taken to be missing from all gymnosperms and from many angiosperm orders and families, although it is not missing really, because desiccation tolerance again appears in the seed maturation program, beginning with the gymnosperms.

A central element in the discussion by Oliver *et al.* [1] is the assumption that vegetative desiccation tolerance strategies have been recruited for seed protection programs. From this, they argue, arose vegetative tolerance in some angiosperms, constituting a re-discovery of the adaptation to dry environments, which accompanied geological changes. They document the process by following the genetic complexity, expression and stress-dependent accumulation of a class of proteins, (de)hydrins and rehydrins. Their name conveys the process with which appearance of the hydrins is correlated, but their exact function remains enigmatic: they are typically highly charged and highly soluble, and structural analyses, circular dichroism (CD) spectra and NMR, can best be summarized by the statement that they are highly unorganized and flexible [2,3]. Their counterparts in seeds are termed LEA (late-embryogenesis-abundant) proteins and, in recent years, a growing number of dehydrin relatives in higher plants indicate that they have been recruited for other stress situations apart from desiccation, for example in chilling or salinity stress tolerance [2,4]. Dehydrins, which in corn exist in seeds and disappear during seedling germination, are a constitutive presence in the desiccation-tolerant moss *Tortula ruralis*. Another quality of this moss, shared by many vegetatively desiccation-tolerant species including angiosperms, is the constitutive high concentration of sucrose or sucrose-related carbohydrates. 'Hardening' of the moss by recurring minor stress episodes leads to an increase in (de- and/or re-)hydrin transcripts which are stored in RNPs in the dried state, seemingly for mobilization and translation upon re-hydration. These hydrins constitute complex gene families in the moss as well as in angiosperm genomes. It is assumed that isoforms protect specific, still mostly unknown, processes much like the various classes of heat shock proteins (HSP) with a general function in protein folding that targets different classes of proteins for repair or protection [5]. Thus, pre-existing protection is built in, while the rate of drying influences the degree of protection.

In the moss *Tortula*, and probably in other lower plants, hardening and the synthesis of an abundance of desiccation-specific proteins seems to be independent of the action of the plant growth regulator abscisic acid (ABA), which plays an

Figure 1
An illustration of the remarkable ability for extreme vegetative desiccation tolerance in an angiosperm species: the same plant of *Craterostigma plantagineum* is shown before and after dehydration and again after rehydration. The time scale for the rehydration shown is 12 hours [6].

important role in seed desiccation tolerance. Seed protection by well-documented ABA-dependent and -independent processes includes the abundant presence of a complex set of hydrins with largely unknown functions, some of which are antigenically related to the moss proteins. Equally, moss

Table 1.

An evolutionary view - vegetative desiccation tolerance in plants

Order/	Tolerance characteristics	Developmental complexity	Mechanisms of tolerance
Liverworts/ hornworts/ mosses	Rapid desiccation tolerated; Some protection mechanisms focus on repair mechanisms photosynthetic-apparatus maintained	Anatomically primitive No vasculature	Cell integrity maintained during drying Rehydration leads to damage Rapid recovery Presence of non-reducing sugars, dehydrins and rehydrins appear Pre-stress existence of mRNA in RNPs
Selaginellales, Isoetales, Lycopodiales	Slower desiccation required; photosynthetic-apparatus maintained	Vascular tissues develop Epidermis appears	Scarcity of data
Equisetum/ Ferns	Slow desiccation required	Increasing anatomical and developmental complexity Epidermis appears	Scarcity of data
Gymnosperms	No vegetative desiccation tolerance	Beginning seed desiccation tolerance	Scarcity of data
Angiosperms	(Re)-discovery of vegetative desiccation tolerance	Established seed desiccation tolerance	Transcripts for proteins typical for drying seeds induced in vegetative tissues
Monocots Poaceae Liliaceae	Slow desiccation required Focus on protection of existing structures		Transcripts of unknown function homologous to constitutively expressed moss genes are induced
Dicots Hamamelidaceae Labiatae Gesneriaceae Scrophulariaceae	Photosynthetic-apparatus either maintained or reduced during desiccation		LEA proteins, sugars and oligosaccharides, Dehydrins and rehydrins in complex gene families Tolerance inducible, ABA influence, sugars may be present or inducible Transcription factors, vesicular traffic

Included are major systematic orders of plants in increasing organizational complexity and following plant appearance during evolution. Monocots - plants with a single cotyledon (for example, grasses [Poaceae]; *Sporobolus stapfianus* is a desiccation tolerant species in the Poaceae family); dicots - two cotyledons (for example, *Arabidopsis thaliana*; *Craterostigma plantagineum* is in this class). *Tortula ruralis* is, among the mosses, the best studied desiccation tolerant species. ABA, abscisic acid; LEA, late embryogenesis abundant.

transcripts (mostly expressed sequence tags) with a relationship to the desiccated state are homologous to desiccation-related transcripts in *Craterostigma plantagineum* (a resurrection plant; see Figure 1), which has emerged as a model for angiosperm vegetative desiccation tolerance.

The accumulated physiological, biochemical and sequence information provides a strong argument for the evolutionary sequence of events outlined by Oliver et al. - namely that rapid drying enabled by pre-existing elements in moss has somehow been conserved to allow the utilization of these elements in seed maturation, although here the process in seed plants is now connected to hormonal control. The 're-invention' of vegetative desiccation tolerance in angiosperms then required slow (or slower) drying - utilizing hormonal control, which originally evolved for the seed protection program, in an inducible fashion now dependent on environmental cues. Table 1 attempts to summarize crucial points, following the evolutionary arguments of Oliver et al.; it also emphasizes that because the available dataset is small, analyses of different species in a comparative manner will be necessary to further substantiate the hypothesis.

The paucity of data prevented Oliver et al. [1] from addressing a most interesting question: how is desiccation tolerance controlled? Considering the speciation of angiosperms, which extends maybe 100 or 150 million years into the past, it is highly unlikely that the gene complement between species is fundamentally different. Most genes utilized by the tolerant species should be present in all land plants. The rediscovery of vegetative desiccation tolerance may be based on changes in regulatory circuits and networks rather than on the biochemical hardware that accomplishes the actual tolerance. How deeply rooted are the control mechanisms that prepare mosses to survive the rapid loss of water, and how could seed desiccation tolerance and subsequent angiosperm vegetative tolerance emerge from such mechanisms? As a solution, Oliver et al. [1] suggest genomics-based approaches. With the accelerating facility of DNA manipulation, sequencing representative genomes or proteomes of 'primitive' plants should no longer remain a pipe-dream, given the importance of resistance to water deficit for the productivity of crops. The increasing scarcity of fresh water and increasing competition between human populations and agriculture for this precious resource support such a suggestion.

References

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