Tortula ruralis

Plant Ecology

5460

9/26/00

Tortula ruralis: model for desert survival

Plants have found many ways to defend against extreme droughts. In all cases it involves both protection and repair strategies. Reponses to desiccation by the drought resistant moss *Tortula ruralis* have been tested extensively by researchers to give some indication of how dessert mosses survive the harsh climate of Southern Utah and other arid regions.

Tortula ruralis has developed many specific responses to drought conditions including structural or cellular protection schemes. The phyllidia or leaves of *T. ruralis* have an epidermis layer of only one cell. During drying the plasma membrane within the cell pulls away from the upper and lower surfaces of the cell wall and collects along with the organelles (Singh et al. 1984) to the ends of the cell. The collapse of the protoplasm is accompanied by only a minor structural movement inward of the cell wall, allowing the physical structure to stay relatively intact. Cytoplasm connections are still maintained between adjacent cell walls even in the dry state, helping to maintaining cellular integrity.

Changes do, however, occur within the cells in response to drying, and they are evident upon rehydration. In particular, the organelles are swollen for several hours, as long as 16-20 hours following uptake of water into rapidly dried cells (about one hour) and slowly dried cells (about 12 hours). There is also ample leakage of solutes into the imbibition solution (Dhindsa and Bewley 1977). More leakage occurs following rapid desiccation than following drying at slower rates, indicating that there can be severe cellular membrane or structural adjustments during rapid water loss. The more time there is available for these adjustments to occur, the less damage that is suffered by the moss upon rehydration.

Interestingly *T. ruralis* seem to spend little energy on chemical or molecular defenses to protect the structural features of its cell wall. Sugars are a common defense against freezing temperatures as well as low water conditions. Soluble sugar content, however, does not change during drying or rehydration, sucrose being present at about 10% of dry mass throughout (Bewley et al. 1978). Membrane protectants, such as trehalose (Crowe and Crowe 1992) are not present. Dehydrin, a Late Embryogenesis Abundant (LEA)-type protein whose function in the tolerance of drought is still debatable (Close et al. 1993), is present constitutively within *T. ruralis*, and its synthesis does not increase during slow drying (Bewley et al. 1993). If the presence of dehydrin is related to stress tolerance (Santarius KA 1973) then moss cells must be permanently in a condition to withstand water loss and therefore adapted to the unpredictable desiccation events they experience in the wild.

With daily episodes of drying and rehydration the moss hardens, so that it can better withstand the more rapid desiccation rates. Hardened moss exhibit greater resistance to desiccation and faster recovery to rehydration. The moss seems to increase the concentration of macromolecules in its plasma membrane preventing greater solute loss (Gupta RK 1976) which allows repair mechanisms to quickly increase to full levels. Mosses maintained in the hydrated state for several days tend to deharden (Schonbeck and Bewley 1981b). This demonstrates a survival mechanism allowing mosses to proliferate in some of the driest climates.

Survival of desiccation by the poikilohydric moss *T. ruralis* appears to depend upon a "repair based" mechanism (Bewley and Oliver 1992). That is, there are a few (during slow drying) or no (during rapid drying) protective mechanisms initiated during desiccation, and there are inherent morphological, cellular, and macromolecular characteristics that allow the moss to withstand unpredictable water loss. Some damage occurs though, particularly in response to severe drying regimes, but restitution events are quickly initiated upon rehydration, and the greater the damage, within tolerable limits, from drying, the more substantial is the repair response.

Studies on cellular responses, and particularly those of the protein-synthesis apparatus seem to give the best indication of how desiccation resistant mosses specifically *T. ruralis* survive desiccation. This moss is well adapted to dry environments retaining viability in the dry state for several months or even decades. Early studies showed that the moss can lose water to approximately 20% of its fresh mass within 60-90 min when pieces of the gametophyte are placed over silica gel (Bewley 1972) and then be rehydrated to its undesiccated mass within 60-90 sseconds(Bewley 1973a). When desiccated, the moss can survive being plunged into liquid nitrogen (Bewley 1973b) and return to full photosynthesis within four hours of rehydration. Drying of the moss results in a decline of polysomes, i.e. the number of ribosomes on the mRNA strand, but some are conserved in the dry moss in a potentially active state (Bewley 1973c). This allows the ribosomes to continue translation practically immediately after rehydration. Messenger RNAs that are present in the hydrated control moss are also conserved during and immediately following desiccation (Dhindsa and Bewley 1978) and are translatable in vitro, yielding a large number of polypeptides that can be identified upon separation (Oliver and Bewley 1984d).

Both RNA and protein synthesis resume within the moss very soon after rehydration (Bewley 1973a, Dhindsa and Bewley 1978), and more quickly following slow drying than after rapid drying. This is because upon rehydration of the rapidly dried moss it takes time for those polysomes conserved in the dry state to complete translation, thus delaying the formation of new polysomes. There is no such impediment following slow drying. The increase in RNA synthesis upon rehydration includes that of new mRNAs, and the relative importance of the conserved mRNAs and newly synthesized messages in the continuation of protein synthesis following desiccation. In hydrated control moss, the recruitment of newly synthesized mRNAs into polysomes is balanced with that of preexisting messages, as part of the normal turnover processes. Upon rehydration of both slowly and rapidly dried moss the proportion of conserved messages soon declines, and within two hours of rehydration few are present as all are replaced by newly synthesized messages. This sometimes even occurs within the first hour of rehydration. (Oliver and Bewley 1984b, 1984c, 1984d).

Slower drying rates achieved by placing the moss in atmospheres of declining relative humidities for three to four hours results in the complete loss of polysomes. But, as after rapid drying, the full polysome complement is restored within two hours of rehydration (Gwozdz et al. 1974).

This raises the question as to the fate of the protein-synthesizing complex within the moss as it dries out. It seems that during drying the ribosomes complete translation of the mRNAs, but because of increasing imposition on the initiation process induced by water stress the number of polysomes decline. The ribosomes and mRNAs remain in their native form even in the extreme condition of the dry state and are reutilized upon subsequent rehydration. If the mRNA is not degraded the process obviously is sped up, yet it is unclear how it survives the drought. If the rate of water loss is too fast to permit all the ribosomes from falling off the mRNA some must remain attached even in the desiccated state, since repair takes longer with fast desiccation, the protein synthesizing compound might experience ribonuclease activity. This would degrade to mRNA and slow down response time.

Another indication of the response that *T. ruralis* takes to rapid and slow desiccation comes from studies on respiration and photosynthesis. During slow drying the ATP content of the moss declines precipitously, with very little being present in the dry state. During rapid desiccation, as would be expected, the decline is much less (Bewley and Gwozdz 1975, Krochko et al. 1979). This is an indication of how organic molecules are disrupted when drying is rapid. Upon rehydration, there is a large increase in ATP synthesis within the first hour, with the slowly dried moss resuming or even exceeding control levels of synthesis within minutes. This excessive synthesis seems to be connected to the rapid repair mechanisms of *T. ruralis*. By giving a surge of energy, repair time can be dramatically reduced and vegetative growth can occur.

The recovery and repair of mitochondria presumably takes longer after the more rapid rate of water loss. Full photosynthesis upon rehydration of rapidly dried moss is suppressed more and takes longer to regain the compensation point than in rehydrated slowly dried moss (Schonbeck and Bewley 1981a). Both slow and rapid desiccations show incredible recovery times for some photosynthesis, starting in less than a minute in many cases.

The desiccation tolerant moss *T. ruralis* has based its survival on a few important abilities. By limiting cellular damage during desiccation the moss eases up on its repair needs upon rehydration. Being able to retain its cellular or structural integrity in the dry state allows it to retain within its cell wall many of the macromolecules needed for survival. However, since it does not undergo drying and rehydration without some cellular damage and metabolic breakdowns, repair mechanisms are initiated upon rehydration.

*Table 1**	Rapid Drying	Slow Drying	Rehydration
Protein synthesis	None	None	Resumes
Polysomes	Some	None	Recovery 2-24 hours
mRNA	Present	Present	Synthesis
Ribosomes	Present	Present	Present
Cytoplasmic factors	Present	Present	Present
Respiration	None	None	Resumes
Oxygen consumption	None	None	Exceeds hydrated controls
ATP	Some	None	Synthesis resumed
Photosynthesis	None	None	Resumes 30 seconds to 4 hours
Chlorophyll content	Reduced	Maintained	Recovers
Contents of cell and its membrane:			
Leakage	None	None	Minimal to extensive
Membrane phosphlipids	Unchanged	Unsaturated fatty acid decline	Increased after Slow Drying
Organelle volume	Decline	Decline	Larger than hydrated controls
Sugar content	Unchanged	Unchanged	Unchanged
Amino acid reserves	Unchanged	Unchanged	Unchanged

*Table 1: A summary of the various metabolic responses of the desiccation tolerant moss *Tortula ruralis*.
Rapid Drying is the loss of water within one hour; Slow Drying is in 12 hours. Both are down to about 10-20% water content compared to a hydrated *Tortula ruralis*. Rehydration effects are in the first hour.

References and Bibliography

Bewley JD 1972. The conservation of polyribosomes in the moss *Tortula ruralis* during total desiccation. J Exp Bot 23: 642-698.

Bewley JD 1973a. Desiccation and protein synthesis in the moss Tortula ruralis Can J Bot 51:203-206.

Bewley JD 1973b. The effects of liquid nitrogen temperatures on protein and RNA synthesis in the moss *Turtula ruralis.* Plant Sci Letters 1:303-308.

Bewley JD 1973c. Polyribosomes conserved during desiccation of the moss *turtula ruralis* are active. Plant Physiol 51: 285-288.

Bewley JD, EA Gwozdz. 1975. Plant desiccation and protein synthesis. II. On the relationship between endogenous ATP levels and protein synthesizing capacity. Plant Physiol 55: 1110-1114.

Bewley JD, P Halmer, JE Krochko, WE Winner. 1978. Metabolism of a drought-tolerant and a drought-sensitive moss: respiration, ATP synthesis and carbohydrate status 185-203 *in JH* Crowe, JS Clegg. eds. Dry biological systems. Academic Press, New York.

Bewley JD, MJ Oliver. 1992. Desiccation-tolerance in vegetative plant tissues and seeds: protein synthesis in relation to desiccation and a potential role for protection and repair mechanisms. pp141 - 160 in GN Somero, CB Osmond, CL Bolis. eds. Water and life: comparative analysis of water relationships at the oganismic, cellular and molecular levels. Springer, Berlin.

Bewley JD, TL Reynolds, MJ Oliver. 1993. Evolving strategies in the adaptation to desiccation. pp 193-201 *in* TJ Close, EL Bray. eds. Plant responses to cellular debydration during environmental stress. American Society of Plant Physiologists Bethesda. Md.

Close TJ, RD Fenton, A Yang, R Asghar, D DeMason, DE Crone, NC Meyer, F Moonan 1993 Dehydrin: the protein. pp 104-118 *in* TJ Close. EA Bray, eds. Plant responses to cellular dehydration during environmental stress. American Society of Plant Physiologists. Bethesda. Md.

Crowe JH, LM Crowe. 1992. Membrane integrity in anhydrobiotic organisms toward a method for stabilizing dry cells. pp 85-103 in GN Somero. CB Osmond. CL Bolis. eds. Water and life: comparative analysis of water relationships at the organismic, cellular and molecular levels. Springer, Berlin.

Dhindsa Rs. 1977. Water stress and protein synthesis. V. Protein synthesis, protein stability and membrane permeability in a drought-sensitive and a drought-tolerant moss. Plant Physiol 59:295-300.

Dhindsa Rs. 1977. Messencer RNA is conserved during drying of drought-tolerant *Turtula ruralis.* Proc Natl Acad Sci USA 75:842-846.

Gwozdz EA, JD Bewley, EB Tucker. 1974. Studies on protein synthesis in *Tortula ruralis:* polyribosome reformating following desiccation. J Exp Bot 25: 599-608.

Krochko JE. WE Winner, JD Bewley. 1979. Respiration in relation to adenosine triphosphate content during desiccation and rehydration of a desiccation-tolerant and desiccation-intolerant moss. Plant Physiol 64: 13- 17

Oliver MJ, JD Bewley. 1984a. Desiccation and ultrastructure in bryophytes. pp 91-131 in W Schultze-Motel, ed. Advances in bryology. Vol 2. A. R. Gantner. Vaduz.

Oliver MJ. 1984b. Plant desiccation and protein synthesis. IV. RNA synthesis, stability and recruitment of RNA into protein synthesis during desiccation and rehydration of the desiccation-tolerant moss, *Tortula rurulis.* Plant Physiol 74: 21-25.

Oliver MJ. 1984c. Plant deciccanon and protein synthesis V. Stability of poly A- and Poly A+ RNAs during deciccation and their synthesis upon rehydration in the desiccation-tolerant moss *Tortula ruralis* and the intolerant moss Cratoneuron Filicinum. Plant Physiol 74:923-927.

Oliver MJ. 1984d. Plant deciccanon and protein synthesis VI. Changes in protein synthesis elicited by desiccation of the moss *Tortula ruralis* are effected at the translational level. Plant Physiol 74:923-927.

Santarius Kurt A. 1973. The Protective Effect of Sugars on Chloroplast Membranes during Temperature and Water Stress and its relationship to Frost, Desiccation and Heat Resistance. Planta 113:105-114.

Schonbeck MW, JD Bewley. 1981a. Responses of the moss *Tortula ruralis* to desiccation treatments. I. Effects of minimum water content and rates of dehydration and rehydration. Can J Bot 59: 2698-2706.

Schonbeck MW, JD Bewley. 1981b. Responses of the moss Tortula ruralis to desiccation treatments. II. Variations in desiccation tolerance. Can J Bot 59:2707-2712.

Singh J, BA Blackwell, RW Miller, JD Bewley. 1984. Membrane organization of the desiccation tolerant moss *Tortula ruralis* in dehydrated states. Plant Physiol 75:1075-1079.