

Review

Oxidative stress and its effects during dehydration[☆]

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Abstract

Water is usually thought to be required for the living state, but several organisms are capable of surviving complete dehydration (anhydrobiotes). Elucidation of the mechanisms of tolerance against dehydration may lead to development of new methods for preserving biological materials that do not normally support drying, which is of enormous practical importance in industry, in clinical medicine as well as in agriculture. One of the molecular mechanisms of damage leading to death in desiccation-sensitive cells upon drying is free-radical attack to phospholipids, DNA and proteins. This review aims to summarize the strategies used by anhydrobiotes to cope with the danger of oxygen toxicity and to present our recent results about the importance of some antioxidant defense systems in the dehydration tolerance of *Saccharomyces cerevisiae*, a usual model in the study of stress response.

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1. Review

At present, with the development of genetic technology and cell transplants, the goal to reach is to store cell lines, for years,

on a shelf, rather than in expensive liquid nitrogen freezers. There is great interest in shipping embryonic stem cells from different laboratories around the world. Also in car accidents or during catastrophes, there is a constant need for blood supplies that could be stored and easily moved. This means that cells must be able to survive the freezing and drying steps, which unequivocally damage membranes and proteins. Successful freeze-drying of platelets with a survival of 90% has already been reported (Wolkers et al., 2001). At present, blood platelets are stored in blood banks for a maximum of 5 days after which they are discarded; these cells are not able to withstand refrigeration. On the other hand, the cellular response of plants to water-deficits has both economic and evolutionary

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importance directly affecting plant productivity in agriculture and plant survival in the natural environment. The knowledge of the mechanism of desiccation tolerance should lead to improve technologies in seed storage and the preservation of dry foods and pharmaceutical products.

Dehydration is known to cause severe damage to organisms at the membrane level as well as to their proteins (Anchordoguy et al., 1990; Prestrelski et al., 1993; Potts, 1994). Nevertheless, many organisms are able to survive complete dehydration (anhydrobiosis) and rapidly resume their metabolic activities when they again come in contact with water (Crowe et al., 1992; Hoekstra et al., 2001; Wright, 2001). While “drought tolerance” can be considered as the tolerance to moderate dehydration, down to a moisture content below which there is no bulk cytoplasmic water present (approximately 23% water on a fresh weight basis – Hoekstra et al., 2001), “desiccation tolerance” generally refers to the tolerance of further dehydration, when the hydration shell of molecules is gradually lost.

Anhydrobiotes are found across all biological kingdoms, with baker's yeast, *Saccharomyces cerevisiae*, being a familiar example. More complex animals, for instance, rotifers, tardigrades, and nematodes such as *Aphelenchus avenae*, have also been shown to be anhydrobiotes, as have the cysts of the crustacean *Artemia salina* (Clegg, 2001). Desiccation is a common phenomenon in the reproductive structures of green plants: pollen, spores and seeds. However, the ability to survive vegetative desiccation is a demonstrable albeit uncommon occurrence in the plant kingdom (Bewley and Krochko, 1982; Ingram and Bartels, 1996; Oliver et al., 2000). As examples we have the angiosperm *Craterostigma plantagineum*, a “resurrection” plant (Bartels and Salamini, 2001), and the bryophyte *Tortula ruralis* (Bewley, 1973; Oliver et al., 2004). In nature, anhydrobiosis often bridges periods of adverse conditions. An explanation would be that, at extreme states of dehydration, anhydrobiotes show great tolerance to physical extremes, including high-energy radiation, immersion in organic solvents, brief exposure to temperatures in excess of 100 °C, and prolonged exposure to very low temperatures (Crowe, 1971; Womersley, 1981). These characteristics increase our interest in the factors which make life without water possible.

Drying is generally considered as the removal of water and, until recently, little attention was given to the oxidative stress that occurs during the process. Very little was known about the damage caused by dehydration due to an increase in the oxidative state of cells. Our knowledge went little beyond the fact that biological systems must be dried under vacuum in order to preserve the leavening capacity of the product.

Although evolution has turned oxygen into a vital compound for aerobic organisms, it can also, when in excess, have very deleterious effects. Chemical injury, in the form of free radical damage, has been suggested by most researchers as one of the major culprits in desiccation injury. Water stress increases the formation of reactive oxygen species (ROS) resulting in lipid peroxidation, denaturation of proteins and nucleic acid damage with severe consequences on overall metabolism (Hansen et al., 2006). A more rapid aging process and diseases such as cancer, Alzheimer, Parkinson and other neurological diseases, seem to

be a clear result of oxidative stress (Willcox et al., 2004). Protection against such damage is mediated, in part, by radical and peroxide scavenging enzymes and by the antioxidant molecules within the cells (Finkel and Holbrook, 2000). Yet more needs to be known about this protection. During drying, different mechanisms of protection appear to act at different stages of water loss. The survival strategy, during early dehydration, seems to be avoiding protein unfolding and membrane disturbances. Upon further removal of water, sugar molecules have to replace this water at hydrogen bonding sites, in order to preserve the native structure of proteins and the correct spacing between phospholipids (Bewley, 1973; Crowe et al., 1992). Meanwhile, clearly, production of free radicals is reduced by down-regulation of metabolism and activation of scavenging mechanisms (Hoekstra et al., 2001).

Maintenance of life, in the absence of water, requires a complex and finely tuned set of mechanisms working in close coordination. In addition to what we have already mentioned, the role played by late embryogenesis abundant proteins (LEA; Hoekstra et al., 2001) and by heat shock proteins (HSPs; Pereira et al., 2001), should not be overlooked. Although the exact functional role of LEA proteins has yet to be determined, several functions have been proposed for them, including acting as molecular chaperones, hydration buffers, membrane stabilizers, and an ion sink (Alsheikh et al., 2003; Crowe et al., 1992). Other kinds of proteins that seem to contribute to cellular stability in anhydrobiotic organisms are the HSPs (Liang et al., 1997a,b). The most important mechanism by which HSPs protect cells from various stresses has traditionally been considered the protein chaperone function. However, HSPs have also been implicated in the inhibition of apoptosis (Beere and Green, 2001; Concannon et al., 2003) and in oxidative damage (Gill et al., 1998; Collins and Clegg, 2004). Recent experiments using human embryonic kidney (293H) cells transfected with the gene for the stress protein p26 from *Artemia* showed a sharp increase in survival during air-drying (Ma et al., 2005).

Most probably, not all of these defenses are turned on, at all times. Organisms have probably developed a defined combination of these mechanisms when in need for protection. It is important to understand the integrated physiological and biochemical interplay in dehydration tolerance of different cells or organisms, in order to apply this knowledge for further, medical and biotechnological, benefits.

1.1. Sources of oxidative stress during dehydration

Aerobic organisms use oxygen as an electron acceptor. However, during respiration, it can be partially reduced, forming ROS, such as superoxide anions ($\cdot\text{O}_2^-$), hydrogen peroxide (H_2O_2) and hydroxyl radical ($\cdot\text{OH}$). Evidence suggests that mitochondria convert 1–2% of the oxygen consumed into $\cdot\text{O}_2^-$ (Boveris and Chance, 1973). These species can cause significant cellular stress and damage; thus, antioxidant protection is essential for survival under aerobic environment. The balance between ROS production and cell defenses determines the degree of oxidative stress.

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