
Commentary

Constraints of tolerance: why are desiccation-tolerant organisms so small or rare?

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Summary

Drying to equilibrium with the air kills nearly all animals and flowering plants, including livestock and crops. This makes drought a key ecological problem for terrestrial life and a major cause of human famine. However, the ability to tolerate complete desiccation is widespread in organisms that are either <5 mm long or found mainly where desiccation-sensitive organisms are scarce. This suggests that there is a trade-off between desiccation tolerance and growth. Recent molecular and biochemical research shows that organisms tolerate desiccation through a set of mechanisms, including sugars that replace water and form glasses, proteins that stabilize macromolecules and membranes, and anti-oxidants that

counter damage by reactive oxygen species. These protections are often induced by drying, and some of the genes involved may be homologous in microbes, plants and animals. Understanding how mechanisms of desiccation tolerance may constrain growth might show how to undo the constraint in some economically important macroorganisms and elucidate the much-studied but elusive relationship between tolerance of stress and productivity.

Key words: animal, desiccation, drought, growth, microbe, plant, productivity, tolerance, trade-off.

Introduction

“We find an Instance here, that Life may be suspended and seemingly destroyed; that... the Circulations may cease, all the Organs and Vessels of the Body may be shrunk up, dried, and hardened; and yet... all the animal Motions and Faculties may be restored, merely by replenishing the Organs and Vessels with a fresh supply of Fluid.”

In these certain terms, Henry Baker announced to the Royal Society in 1743 that some animals could tolerate complete desiccation: they could dry to equilibrium with the air and then resume normal function upon rehydration (Keilin, 1959). Baker's 'Instance' was the larva of the nematode *Anguillulina tritici*, and his certainty was well placed. Desiccation tolerance has been confirmed in nematodes and in the rotifers observed by van Leeuwenhoek in 1702 (Keilin, 1959) and discovered in four other phyla of animals, in some algae, fungi and bacteria, in ~350 species of flowering plants and ferns and in most bryophytes, lichens and seeds of flowering plants (Table 1). Many desiccation-tolerant species can survive in a dry state for years, and some for decades (Alpert and Oliver, 2002; Guidetti and Jonsson, 2002).

The discovery that a nematode could lose virtually all its free

internal water without dying was remarkable because most animals and plants die instantly if their cells equilibrate with even moderately dry air. Water maintains the structure of intracellular macromolecules and membranes; removing water from the cells of desiccation-sensitive organisms irreversibly aggregates essential macromolecules and disintegrates organelles. This makes drought – lack of water in the environment – one of the greatest obstacles to the survival of animals and plants on land. Desiccation-sensitive organisms tolerate drought by maintaining a chronic disequilibrium between internal water content and external water availability. Desiccation-tolerant organisms tolerate drought by drying up but not dying.

Desiccation tolerance is remarkable also because it means that an organism must be able to suspend animation. Since metabolism requires that enzymes and membranes be surrounded by water, desiccation-tolerant cells must be able to cease metabolism and then start it again, as Baker proposed. Metabolism probably stops by the time a cell has dried to about 0.1 g H₂O g⁻¹ dry mass, because this probably leaves too little water to form a monolayer around proteins and membranes (Clegg, 1973; Billi and Potts, 2002). Drying to 10% absolute water content is roughly equivalent to equilibration with air of 50% relative humidity at 20°C and to dropping to a water

Table 1. *The taxonomic range of desiccation tolerance*

Group	Known occurrence	Selected references
Nematodes	Many species	Wharton (2003); Treonis and Wall (2005)
Rotifers	Many species, including most species tested in the order Bdelloidea	Ricci and Caprioli (2005)
Tardigrades	Many species	Wright (2001); Jönsson and Järemo (2003)
Crustaceans	Encysted embryos of several genera of anostracans, including brine and fairy shrimps	Mitchell (1990); Clegg (2005)
Arthropods	Larva of the fly <i>Polypedilum vanderplanki</i>	Watanabe et al. (2004); Kikawada et al. (2005)
Lichens	Most species tested	Kappen and Valladares (1999)
Yeasts	Some species	Garay-Arroyo et al. (2000)
Other fungi	Some species	Mazur (1968)
Mosses	Most species tested	Proctor and Tuba (2002)
Liverworts	Many species	Proctor and Tuba (2002)
Pteridophytes	Perhaps 50 species as sporophytes, probably many as spores, some as gametophytes	Pence (2000); Porembski and Barthlott (2000)
Gymnosperms	No adults but some seeds and pollen	Porembski and Barthlott (2000); Dickie and Prichard (2002); Hoekstra (2002)
Angiosperms	About 300 species as adults, over 95% of species as seeds, perhaps most pollen	Porembski and Barthlott (2000); Hoekstra (2002); Tweddle et al. (2003)
Bacteria	Many species, including cyanobacteria	Billi and Potts (2002); Buedel et al. (2002); de la Torre et al. (2003)
Terrestrial microalgae	Many species	Trainor and Gladych (1995)
Marine macroalgae	The intertidal red alga <i>Porphyra dentata</i>	Abe et al. (2001)

potential of -100 MPa. These thresholds also clearly separate desiccation-sensitive from -tolerant species (Alpert, 2005): there is a gap in the minimum water contents that different living things can survive. Except for a small proportion of seeds (Tweddle et al., 2003), almost all species tested either die if dried to 20% water content, and are thus desiccation-sensitive, or survive drying to 10% water content and thus tolerate desiccation.

It should be noted that 'desiccation tolerance' has sometimes been used to mean tolerance of partial desiccation by organisms that die if they desiccate completely, as in the literature on insects and intertidal algae. Here, the term will be used to mean tolerance of complete desiccation, defined as drying to equilibrium with moderately to very dry air, or to 10% water content or less.

A prime secret of desiccation tolerance appears to be sugars (Alpert and Oliver, 2002). Certain sugars, mainly non-reducing disaccharides, may take the place of water in preventing the aggregation of macromolecules and the disintegration of membranes as cells dry. Many tolerant plants accumulate high concentrations of the familiar disaccharide sucrose (Vicre et al., 2004a). Many desiccation-tolerant animals and microbes and also some plants synthesize the disaccharide trehalose (Wingler, 2002; Breeuwer et al., 2003; Elbein et al., 2003; Crowe et al., 2005). In tandem with specific proteins (Goyal et al., 2005b), these sugars probably stabilize drying cells both by direct interaction with macromolecules and membranes and by reversibly immobilizing cytoplasm in an extremely slow-flowing liquid, a glass (Buitink and Leprince, 2004). Interestingly, sugar glasses also tend to form at the threshold of 10% water content, at least in seeds (Walters et al., 2005).

Researchers have put the secret of sugars to medical use. Incubation in trehalose can induce desiccation tolerance in human blood platelets (Crowe et al., 2005). Genetically modifying desiccation-sensitive, single cells to produce their own trehalose can also confer tolerance of brief periods of desiccation (Billi et al., 2000; Guo et al., 2000). However, these methods have not worked on whole plants or metazoans (Alpert, 2005), probably because they require a set of mechanisms to tolerate desiccation: sugars are not the sole secret of tolerance (Oliver et al., 2001; Potts, 2001; Rascio and La Rocca, 2005). Since some rotifers tolerate desiccation without accumulating sugars, they are not a *sine qua non* of tolerance either (Tunnacliffe and Lapinski, 2003).

The taxonomic scope of desiccation tolerance in plants and animals is now fairly well known, and the genetic and biochemical mechanisms of tolerance are becoming clear. What remains a mystery is why desiccation tolerance is not more common. Over 260 years after Baker's report, most people and many scientists are still surprised to learn that any animals or plants can dry up without dying. This is probably because desiccation-tolerant animals and plants are surprisingly inconspicuous. It appears that none of the animals that humans use for food tolerate desiccation, nor do any of the plants used for food or construction, except as seeds. No trees and very few shrubs are reported to tolerate desiccation. No known desiccation-tolerant animals exceed 5 mm in length, and almost all are microscopic. Although desiccation-tolerant animals and plants occur on all continents, they appear to form a minor element of the fauna and flora except in the driest habitats (Fig. 1). About 90% of the tolerant flowering plants are largely relegated to tropical rock outcrops (Porembski and Barthlott, 2004). The one known place where desiccation-tolerant animals

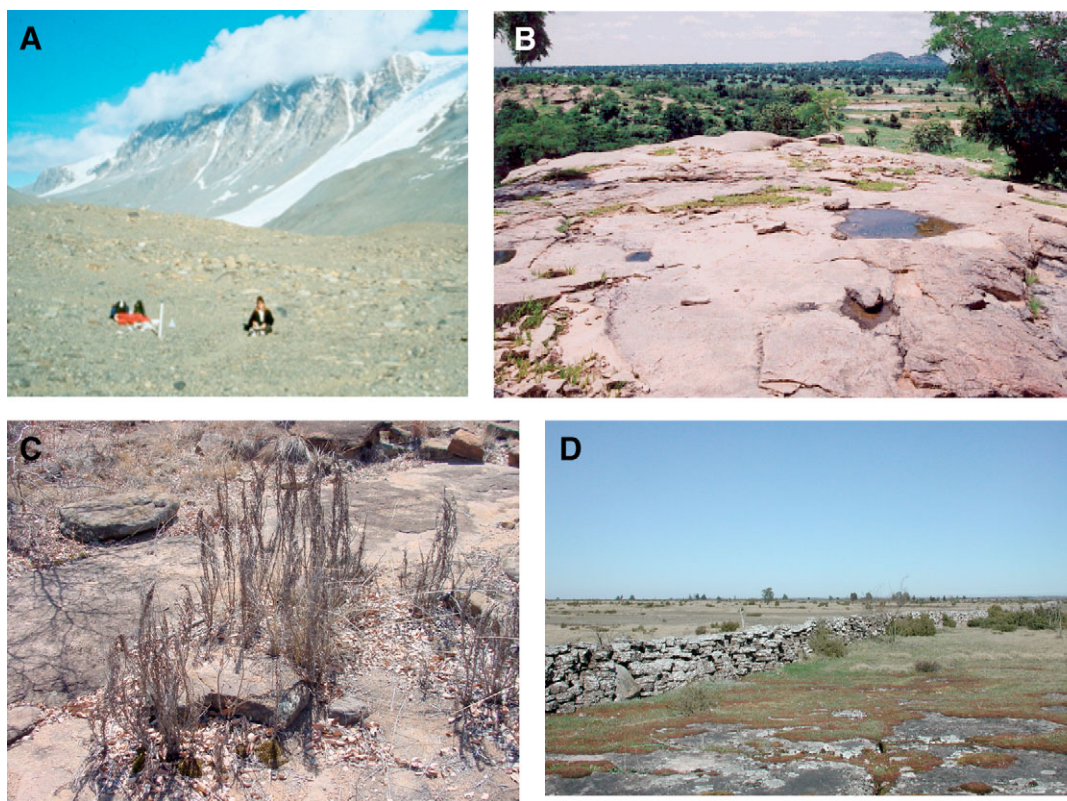


Fig. 1. Desiccation-tolerant animals and flowering plants are dominant species in some extremely dry habitats: (A) Taylor Valley, Antarctica, where the tolerant soil nematode *Scottnema lindsayae* may be the most common animal; (B) seasonally dry, ephemeral pools in Nigeria, the habitat of the tolerant larva of the fly *Polypedilum vanderplanki*; (C) rock outcrops in South Africa, a habitat of the tolerant shrub *Myrothamnus flabellifolius*. In less dry habitats, desiccation-tolerant animals and plants are subordinate species: (D) temperate heathland in Öland, Sweden, a habitat of the tardigrade *Richtersius coronifer*. Photos by Andy Parsons (A), Takashi Okuda (B), Jill Farrant (C) and Ingemar Jönsson (D).

may outnumber sensitive ones is in the Dry Valleys of Antarctica (Treonis and Wall, 2005). If desiccation tolerance solves what may be the greatest problem of living on land, why are terrestrial, desiccation-tolerant organisms so small or rare?

The problem of size

Desiccation-tolerant animals may be small because of the physical stresses associated with drying (Table 2). Animal cells shrink as they dry, and the whole animal must shrink with them. All animals that tolerate desiccation as adults adopt distinctive, balled or curled shapes as they dry (Fig. 2). Rigid external or internal skeletons could prevent this, and none of these animals have skeletons. In the tolerant animals that do have exoskeletons, tolerance is restricted to juvenile stages before skeletons form (Fig. 3). It would be interesting to know whether there is generally a developmentally programmed acquisition and loss of tolerance at the cellular level in these animals, as there is in most seeds, or whether individual cells remain tolerant in some adult animals.

Plants show greater ability than animals to combine tolerance and rigidity. The leaves of desiccation-tolerant plants often curl or fold as they dry, but the stems may remain straight and change little in length (Fig. 4). This may be

possible because each plant cell has its own exoskeleton, a rigid cell wall; physical stress probably does not compound across groups of cells as readily in plants as in animals. Some tolerant plants do show various specialized traits that reduce the shrinkage of cells away from their walls or increase the ability of the wall to fold or bend as the cell shrinks (Table 2).

The height of desiccation-tolerant plants may be constrained by a different factor: ability to re-establish upward movement of water in stems after desiccation and rehydration (Schneider et al., 2000). Root pressure and capillary action cannot refill xylem above ~3 m, and this is also about the maximum height of tolerant plants.

The need to lose water freely during desiccation may restrict the thickness of desiccation-tolerant organisms (Table 2). Rate of desiccation affects the survival of many tolerant organisms. Rapid drying may preclude induction of mechanisms needed for tolerance (Ricci et al., 2003; Clegg, 2005), and one function of contraction and other behavioral responses to desiccation in animals may be to slow drying (Kikawada et al., 2005). However, very slow drying may prolong the time spent at water contents just above those at which metabolism ceases, and these water contents may be particularly damaging (Berjak and Pammenter, 2001; Proctor, 2003; Walters et al., 2005). A

specific mechanism to facilitate the loss of water from cells during drying may be upregulation of aquaporins that increase the permeability of membranes (Table 2).

The question of productivity

Three lines of evidence suggest that desiccation-tolerant species may be rare because tolerance decreases growth rate.

First, genetic and evolutionary evidence indicates that desiccation tolerance is a primitive character that has been lost in lineages that evolved mechanisms to resist desiccation or that moved into habitats where they were not subject to desiccation. Retention of unexpressed genes for tolerance in some of these organisms argues that tolerance may have been selected against, rather than just no longer selected for. Second, the few studies of ecological patterns in desiccation tolerance

Table 2. Problems caused by desiccation and mechanisms of desiccation tolerance

Problem	Mechanism	Selected references
Mechanical damage due to shrinkage	In plants, changes in cell wall composition that increase flexibility	(Jones and McQueen-Mason, 2004; Viret et al., 2004b)
	In plants, folding cell walls	(Vander Willigen et al., 2004)
	In plants, replacement of water in vacuoles by non-aqueous compounds and fragmentation of vacuoles	(Farrant, 2000; Viret et al., 2004a)
Physiological damage at low intermediate water contents	Upregulation of proteins that increase membrane permeability	(Smith-Espinoza et al., 2003; Vander Willigen et al., 2004)
Disintegration of membranes and aggregation of macromolecules during drying, coalescence of lipid bodies and membrane leakage upon rehydration	Accumulation of sugars, especially non-reducing disaccharides, that stabilize molecules, depress temperature (T_m) of membrane phase change from liquid crystal to gel, and form glasses with high melting temperature (T_g)	(Wingler, 2002; Bernacchia and Furini, 2004; Buitink and Leprince, 2004; Crowe et al., 2005)
	LEA proteins, which act as molecular chaperones and interact with sugars to form glasses	(Wise and Tunnacliffe, 2004; Goyal et al., 2005a; Oliver et al., 2005)
	Partitioning of amphiphiles into membranes	(Hoekstra and Golovina, 2002; Oliver et al., 2002)
	Small stress proteins, which may act as chaperones or repair damage upon rehydration	(Collins and Clegg, 2004; Crowe et al., 2005; Potts et al., 2005)
	Changes in lipid composition that stabilize membranes, such as increases in phospholipids, degree of saturation, and free sterols	(Quartacci et al., 2002; Hoekstra, 2005)
	In seeds, oleosins	(Murphy, et al., 2001)
Generation of reactive oxygen species (ROS)	Synthesis of antioxidants during drying, maintenance of pools of reduced antioxidants and ROS-scavenging enzymes	(Shirkey et al., 2000; Augusti et al., 2001; Espindola et al., 2003; Kranner and Birtic, 2005)
	In plants, downregulation of photosynthesis early in drying	(Jensen et al., 1999; Deng et al., 2003; Hirai et al., 2004; Illing et al., 2005)
	In plants, folding of leaves	(Farrant et al., 2003)
	Programmed chlorophyll loss	(Tuba et al., 1996)
Triggering of cell death by oxidized glutathione	Rapid reduction of glutathione upon rehydration	(Kranner and Birtic, 2005)
In plants, disintegration of the photosynthetic apparatus	Modification of proteins in PSII	(Peeva and Maslenkova, 2004)
Accumulation of damage from UV and gamma radiation and from Maillard and Fenton reactions while dry	UV-absorbing pigments	(Potts, 1996)
	DNA repair	(Wilson et al., 2004)
In plants, cavitation of xylem	DNA protection	(Potts et al., 2005)
	Height <3 m, low hydraulic conductivity	(Sherwin et al., 1998)
	Drying too fast for induction of tolerance mechanisms	(Kikawada et al., 2005)
In animals, contraction, construction of larval tube by <i>Polypedilum</i>	In animals, contraction, construction of larval tube by <i>Polypedilum</i>	(Kikawada et al., 2005)
	In plants, signaling for induction of tolerance mechanisms via ABA	(Beckett et al., 2000; Bartels and Salamini, 2001)

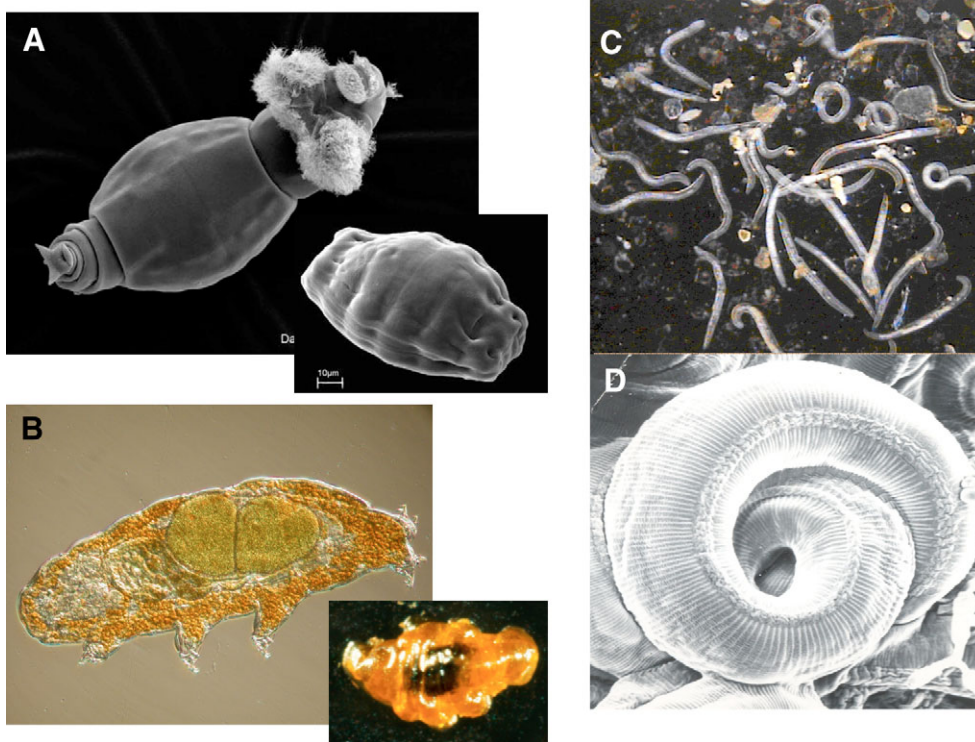


Fig. 2. Adult animals in three phyla tolerate desiccation; all ball or curl up as they dry: (A) scanning electron micrographs (SEMs) of the rotifer *Macrotrachela quadricornifera* hydrated (length 0.2 mm) and desiccated; (B) light micrograph and photo of the tardigrade *Richtersius coronifer*; (C) active adults of the nematode *Scottnema lindsayae* (50 \times); (D) SEM (1600 \times) of a desiccated nematode, *Acrobeloides* sp. Photos by Giulio Melone (A), Ingemar Jönsson (B), Amy Treonis (C) and Diana Wall (D).

are consistent with the hypothesis that tolerant species are poor competitors. Tendency for desiccation-sensitive species to replace desiccation-tolerant ones along gradients of increasing water availability could be due to faster growth and reproduction of sensitive species in habitats where sensitive species can survive. Third, mechanisms of tolerance appear likely to constrain growth. Some mechanisms may conflict with resource acquisition and others may require the allocation of resources away from growth.

Selection against tolerance?

Tolerance of desiccation may be a very ancient trait in living things. Phylogenetic analyses and comparative surveys suggest that tolerance is an ancestral character in land plants or their spores (Oliver et al., 2005) and in bdelloid rotifers (Ricci, 1998). Late embryogenesis abundant (LEA) genes, named after their association with the onset of desiccation tolerance in seeds, have been found in tolerant mosses, bacteria, yeasts, nematodes and possibly algae (Li et al., 1998; Garay-Arroyo et al., 2000; Alpert and Oliver, 2002; Wise and Tunnacliffe, 2004). Some LEA genes appear to be homologous in microbes, plants and animals (Wise and Tunnacliffe, 2004). This suggests that desiccation tolerance evolved before the divergence of these kingdoms or that the genetic potential for tolerance is extremely widespread among organisms. In either case, it is the absence, more than the presence, of tolerance that demands explanation.

There is evidence from plants that desiccation tolerance is lost when organisms are no longer subject to desiccation, even when the genes for tolerance are still present. Tolerance in

adult land plants may have been lost when the evolution of vascular water transport from roots to shoots permitted adults to resist desiccation (Oliver et al., 2005). Tolerance was conserved in seeds and spores, which were still subject to desiccation, and the genes needed for desiccation tolerance may be present in most desiccation-sensitive adult plants but either not expressed or recruited to other functions (Bartels and Salamini, 2001; Zeng and Kermodé, 2004). This may explain why plants have apparently been able to re-evolve tolerance at

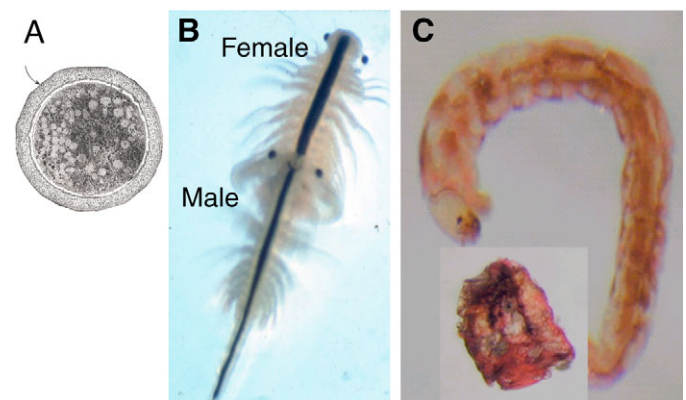


Fig. 3. In animals that have skeletons as adults, desiccation tolerance is restricted to juvenile stages: (A) SEM of a tolerant, encysted gastrula (diameter, 0.2 mm) of the brine shrimp *Artemia franciscana*; (B) desiccation-sensitive, adult *A. franciscana* (length ~1 mm); (C) active and desiccated larvae of the fly *Polypedilum vanderplanki*. Photos by James Clegg (A,B) and Takashi Okuda (C).

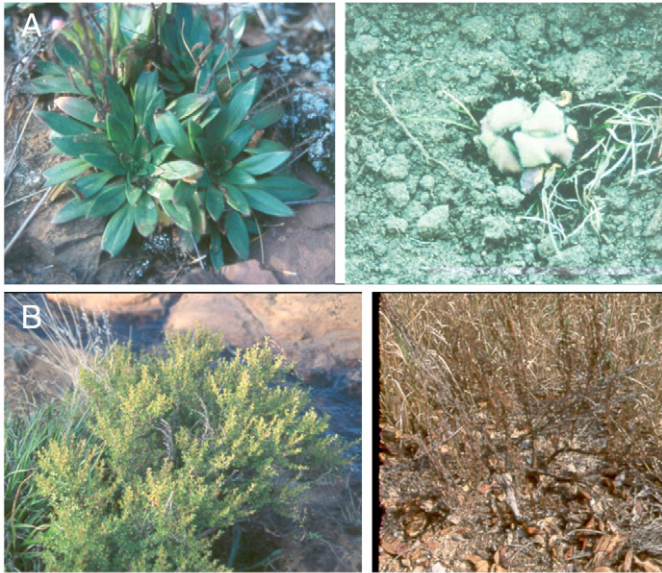


Fig. 4. Leaves of the desiccation-tolerant, herbaceous plant *Craterostigma wilmsii* curl as they dry (A). However, woody stems of the tolerant shrub *Myrothamnus flabellifolius* change little in shape (B). Photos by Jill Farrant.

least 12 times (Illing et al., 2005; Oliver et al., 2005). Selection for re-evolution may have occurred as various lineages spread into extremely dry habitats where they could not resist desiccation, such as onto rock outcrops in the tropics (Porembski and Barthlott, 2000). Re-evolution of tolerance in adults may be mainly a matter of changes in regulatory genes (Bartels and Salamini, 2001) and thus a case of evolution of development.

There is some evidence for selection on desiccation tolerance in animals, mainly rotifers and tardigrades. The bdelloid rotifers that have lost desiccation tolerance are all fully aquatic, although not all aquatic species are sensitive (Ricci, 1998). A model of survival and reproduction of intertidal tardigrades found that the evolution of tolerance depended upon whether sensitive animals experience lethal desiccation (Jönsson and Järemo, 2003). Other theoretical considerations (Jönsson, 2005) and empirical comparisons (Ricci and Caprioli, 2005) suggest that low fecundity is associated with tolerance. These reports are at least consistent with loss of desiccation tolerance when animals can avoid desiccation.

Tolerance versus competitiveness?

The relative dearth of desiccation-tolerant organisms in habitats where water availability is high (Alpert, 2005) could be due to competition with desiccation-sensitive organisms, if there is a trade-off between tolerance and competitive ability. Apparent trade-offs between tolerance and relative competitive ability have been reported in systems as diverse as tolerance of disturbance by microbes (Buckling et al., 2000), tolerance of high temperature by ants (Bestelmeyer, 2000) and tolerance

of salinity and drought by plants (Crain et al., 2004; Liancourt et al., 2005). There seem to have been no direct tests for a trade-off between competitive ability and desiccation tolerance, but there is a small amount of indirect evidence for such a trade-off in plants: succession from tolerant algae to sensitive plants in lakes after stabilisation of the water level (Van Geest et al., 2005) and apparent niche partitioning between flowering plants that differ in desiccation tolerance (Heilmeyer et al., 2005).

A plausible reason for competitive inferiority of desiccation-tolerant organisms could be a trade-off between tolerance and growth or reproduction. Competitive ability is often positively associated with productivity, and maximum rate of growth or reproduction is often negatively associated with different types of tolerance or resistance, such as salt, drought and shade tolerance in plants (Houle, 2002; Silvertown, 2004), resistance to herbivory (Prittinen et al., 2003), cadmium tolerance in fish (Xie and Klerks, 2004), immune response in birds (Ardia, 2005) and resistance of tadpoles to predators (Relyea and Auld, 2005). There appear to have been no direct tests for a trade-off between desiccation tolerance and productivity in either animals or flowering plants, but there are a few preliminary tests from mosses. Of two arctic stream mosses, the more desiccation-tolerant moss showed a lower maximum rate of photosynthesis and less increase in growth in response to the addition of a limiting nutrient (Arscott et al., 2000). Of two other mosses, the more tolerant was less productive (Bates and Bakken, 1998).

Possible mechanistic conflicts between tolerance and productivity

Although negative association between traits such as desiccation tolerance and productivity can point to trade-offs, knowledge of the mechanisms that underlie these associations is needed to confirm trade-offs (Restif and Koella, 2004). Growing understanding of the mechanisms of tolerance suggests that desiccation tolerance and productivity might show two common types of trade-off (Angilletta et al., 2002): avoidance of mortality *versus* acquisition of resources, and allocation of resources between competing functions.

At least five mechanisms of tolerance (Table 2) seem likely to conflict with rate or time available for resource acquisition: inducible shutdown of metabolism, recovery after rehydration, decreased membrane fluidity, hormonal mediation, and reduced threshold for cavitation, i.e. the formation of gas-filled spaces that interrupt water flow in the xylem of plants. Because different components of metabolism differ in their sensitivity to desiccation, damaging metabolic imbalances can occur during drying. For instance, interruption of electron transport chains and of transfer of absorbed light energy to photosynthesis generate reactive oxygen species (ROS), which can destroy virtually all cell components (Kranmer and Birtic, 2005). Together with the need to induce protection against loss of proteins and membranes, this may be why various tolerant plants begin to shut down metabolism early in drying (Collett et al., 2003; Hirai et al., 2004; Illing et al., 2005), at the expense of time available for growth.

Recovery of function after desiccation and rehydration also takes time away from growth, particularly in vascular plants. Time for recovery varies from minutes in some mosses that have been dry for a few days to about an hour in the larva of *Polypedium* and about 1–2 days in most flowering plants (Alpert, 2000; Kikawada et al., 2005). The effectiveness of some protections against damage during desiccation appears to trade off against rate of recovery. For example, programmed chlorophyll loss may be a very effective protection against the absorption of excess light energy but slow recovery of photosynthetic capacity (Sherwin and Farrant, 1996; Tuba et al., 1996). One disadvantage of desiccation tolerance in seeds is slow germination and establishment compared with sensitive seeds (Tweddle et al., 2003).

In at least some mosses and flowering plants, the hormone abscisic acid (ABA) serves as a signal for induction of desiccation tolerance (Beckett et al., 2000; Bartels and Salamini, 2001). Since ABA also tends to slow growth in plants (Farnsworth, 2004), this may build in a conflict between tolerance and growth. There is evidence for such a conflict in ABA-mediated differences in drought tolerance and reproductive output in desiccation-sensitive plants (Heschel and Hausmann, 2001). Other hormones with multiple effects are known to mediate trade-offs in animals, such as between resistance to parasites and breeding behavior in birds (Mougeot et al., 2005) and between flight capability and early fecundity in crickets (Zera and Zhao, 2004). However, there seems to be no research yet on the potential role of hormones in desiccation tolerance in animals.

Survival at low levels of resource availability is sometimes negatively associated with maximum rate of resource use and therefore of growth in both plants and animals (Sack et al., 2003; Heideman et al., 2005; Hoffmann et al., 2005). For example, some shade-tolerant plants have a low rate of respiration (Sack et al., 2003), which reduces both likelihood of exhausting reserves in low light and rate of growth in high light. A low rate of respiration in desiccation-tolerant organisms could decrease generation of ROS by mitochondria during drying and rehydration (Hoekstra, 2005) but also limit rate of growth. Deterioration of membranes appears to limit the time that various tolerant organisms can survive in the dry state (Hoekstra, 2005), and long survival is associated with a high degree of saturation of fatty acids in membranes (Table 2). This can decrease membrane mobility, which may both stabilize membranes and limit the rate of membrane transport and cellular growth (Hoekstra, 2005); another advantage of having highly saturated fatty acids may be that polyunsaturated ones are more liable to oxidation. One mechanism for a trade-off between minimum water requirements and maximum water use in plants is diameter of xylem vessels. Large vessels conduct more efficiently and permit more rapid growth but are also more subject to cavitation during drought. There is evidence for a trade-off between efficiency and safety in some plant species, with populations from drier habitats having smaller vessels (Verheyden et al., 2005). Hydraulic conductivity in the desiccation-tolerant shrub *Myrothamnus*

flabellifolius is among the lowest reported in angiosperms (Sherwin et al., 1998), suggesting that desiccation tolerance in plants may trade off against efficiency of water transport.

At least four mechanisms of desiccation tolerance could allocate resources away from growth: accumulation of sugars, synthesis of proteins, upregulation of antioxidants, and the need to repair damage accumulated while dry (Table 2). Sugars may accumulate to very high levels. For example, sugars associated with desiccation tolerance can make up over 40% of the mass of the tolerant plant *Craterostigma plantagineum* (Norwood et al., 2003; Bartels, 2005). In some tolerant species, desiccation induces the expression of hundreds of genes, including LEA genes, whose proteins may act as chaperones for other proteins and interact with sugar to immobilize dry cytoplasm (Goyal et al., 2005a), and small stress proteins that can increase the effectiveness of LEA proteins and trehalose (Crowe et al., 2005; Ma et al., 2005). Antioxidants such as glutathione and enzymes that scavenge ROS such as superoxide dismutase are a major defense against ROS in desiccation-tolerant organisms (Shirkey et al., 2000; Kranner and Birtic, 2005).

The synthesis of these sugars, proteins and antioxidants could subtract from energy and resources available for growth. There is evidence that cycles of desiccation and rehydration deplete energy resources in tardigrades and nematodes (Jönsson, 2005), although this does not seem to be true in rotifers (Ricci and Caprioli, 2005), whose fecundity may actually decrease when they are not subjected to cycles of drying. There has apparently been no work on possible trade-offs between desiccation tolerance and escape from predators, although carotenoids seem to increase immune resistance as ROS scavengers but may increase conspicuousness and hence predation in copepods (Van der Veen, 2005).

Recovery from desiccation is associated with a burst of respiration in mosses and lichens (Alpert, 2000); this may be both a symptom of damage and requirement for repair. Mosses may rely more heavily upon repair for tolerance than most organisms (Oliver et al., 2000), but all tolerant organisms are subject to damage to DNA and other cell components from radiation and have limited or no ability to repair the damage until metabolism restarts. The need for effective repair mechanisms may help explain the high tolerance of some tardigrades and bacteria to both desiccation and radiation (Cox and Battista, 2005; Jönsson, 2005). In environments where an organism must tolerate desiccation to survive, loss of potential for growth due to allocation of resources away from growth to mechanisms of tolerance may be relatively unimportant. However, if there is a trade-off between rapid growth and tolerance, selection for growth might favor loss of tolerance in environments where desiccation can be avoided.

Conclusions

Although physical constraints may explain why desiccation-tolerant animals are small, physiological ones may explain why

desiccation tolerance is not more common. There is ample reason to suspect that tolerance of desiccation by animals and plants may constrain their growth and reproduction. However, there have been almost no direct tests for association between high tolerance and low productivity or competitive ability, or for effects of mechanisms of tolerance on growth or reproduction. Research on animals has been especially lacking. One scientific reason for pursuing this research now is to elucidate the relationship between tolerance and growth. One societal reason is that understanding the basis for trade-offs between desiccation tolerance and productivity might allow genetic engineers to at least partly uncouple tolerance from slow growth and to engineer tolerant, productive crops. For example, it might be relatively simple to bypass ABA as a mechanism for induction of tolerance and avoid its tendency to slow growth (Bartels and Salamini, 2001). In a recent effort to improve crop production in Ethiopia, high-yielding varieties of barley were developed (Sinebo, 2005). However, they outgrew traditional varieties only in years when water was plentiful, i.e. in the absence of drought.

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References

- Abe, S., Kurashima, A., Yokohama, Y. and Tanaka, J. (2001). The cellular ability of desiccation tolerance in Japanese intertidal seaweeds. *Botanica Marina* **44**, 125-131.
- Alpert, P. (2000). The discovery, scope, and puzzle of desiccation tolerance in plants. *Plant Ecol.* **151**, 5-17.
- Alpert, P. (2005). The limits and frontiers of desiccation-tolerant life. *Integr. Comp. Biol.* **45**, 685-695.
- Alpert, P. and Oliver, M. J. (2002). Drying without dying. In *Desiccation and Survival in Plants: Drying Without Dying* (ed. M. Black and H. W. Prichard), pp. 3-43. Wallingford, UK: CAB International.
- Angilletta, M. J., Niewiarowski, P. H. and Navas, C. A. (2002). The evolution of thermal physiology in ectotherms. *J. Therm. Biol.* **27**, 249-268.
- Ardia, D. R. (2005). Tree swallows trade off immune function and reproductive effort differently across their range. *Ecology* **86**, 2040-2046.
- Arscott, D. B., Bowden, W. B. and Finlay, J. C. (2000). Effects of desiccation and temperature/irradiance on the metabolism of 2 arctic stream bryophyte taxa. *J. N. Am. Benthol. Soc.* **19**, 263-273.
- Augusti, A., Scartazza, A., Navari-Izzo, F., Sgherri, C. L. M., Stevanovic, B. and Brugnoli, E. (2001). Photosystem II photochemical efficiency, zeaxanthin and antioxidant contents in the poikilohydric *Ramonda serbica* during dehydration and rehydration. *Photosyn. Res.* **67**, 79-88.
- Bartels, D. (2005). Desiccation tolerance studied in the resurrection plant, *Craterostigma plantagineum*. *Integr. Comp. Biol.* **45**, 696-701.
- Bartels, D. and Salamini, F. (2001). Desiccation tolerance in the resurrection plant *Craterostigma plantagineum*: a contribution to the study of drought tolerance at the molecular level. *Plant Physiol.* **127**, 1346-1353.
- Bates, J. W. and Bakken, S. (1998). Nutrient retention, desiccation, and recycling. In *Bryology for the Twenty-first Century* (ed. J. W. Bates, N. W. Ashton and J. G. Duckett), pp. 293-304. Leeds, UK: W. S. Mancy & Son.
- Beckett, R. P., Csintalan, Z. and Tuba, Z. (2000). ABA treatment increases both the desiccation tolerance of photosynthesis, and nonphotochemical quenching in the moss *Atrichum undulatum*. *Plant Ecol.* **151**, 65-71.
- Berjak, P. and Pammenter, N. W. (2001). Seed recalcitrance – current perspectives. *S. Afr. J. Bot.* **67**, 79-89.
- Bernacchia, G. and Furini, A. (2004). Biochemical and molecular responses to water stress in resurrection plants. *Physiol. Plantarum* **121**, 175-181.
- Bestelmeyer, B. T. (2000). The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. *J. Anim. Ecol.* **69**, 998-1009.
- Billi, D. and Potts, M. (2002). Life and death of dried prokaryotes. *Res. Microbiol.* **153**, 7-12.
- Billi, D., Wright, D. J., Helm, R. F., Prickett, T., Potts, M. and Crowe, J. H. (2000). Engineering desiccation tolerance in *Escherichia coli*. *Appl. Environ. Microbiol.* **66**, 1680-1684.
- Breeuwer, P., Lardeau, A., Peterz, M. and Joosten, H. M. (2003). Desiccation and heat tolerance of *Enterobacter sakazakii*. *J. Appl. Microbiol.* **95**, 967-973.
- Buckling, A., Kassen, R., Bell, G. and Rainey, P. B. (2000). Disturbance and diversity in experimental microcosms. *Nature* **408**, 961-964.
- Buedel, B., Poremski, S. and Barthlott, W. (2002). Cyanobacteria of inselbergs in the Atlantic rainforest zone of eastern Brazil. *Phycologia* **41**, 498-506.
- Buitink, J. and Leprince, O. (2004). Glass formation in plant anhydrobiotes: survival in the dry state. *Cryobiology* **48**, 215-228.
- Clegg, J. S. (1973). Do dried cryptobiotics have a metabolism? In *Anhydrobiosis* (ed. J. H. Crowe and J. S. Clegg), pp. 141-146. Stroudsburg, PA: Dowden, Hutchinson and Ross.
- Clegg, J. S. (2005). Desiccation tolerance in encysted embryos of the animal extremophile, *Artemia*. *Integr. Comp. Biol.* **45**, 715-724.
- Collett, H., Butowt, R., Smith, J., Farrant, J. and Illing, N. (2003). Photosynthetic genes are differentially transcribed during the dehydration-rehydration cycle in the resurrection plant, *Xerophyta humilis*. *J. Exp. Bot.* **54**, 2593-2595.
- Collins, C. H. and Clegg, J. S. (2004). A small heat-shock protein, p26, from the crustacean *Artemia* protects mammalian cells (Cos-1) from oxidative damage. *Cell Biol. Int.* **28**, 449-455.
- Cox, M. M. and Battista, J. R. (2005). *Deinococcus radiodurans* – the consummate survivor. *Nat. Rev. Microbiol.* **3**, 882-892.
- Crain, C. M., Silliman, B. R., Bertness, S. L. and Bertness, M. D. (2004). Physical and biotic drivers of plant distribution across estuarine salinity gradients. *Ecology* **85**, 2539-2549.
- Crowe, J. H., Crowe, L. M., Wolkers, W. F., Oliver, A. D., Ma, X., Auh, J.-H., Tang, M., Zhu, S., Norris, J. and Tablin, F. (2005). Stabilization of dry mammalian cells: lessons from nature. *Integr. Comp. Biol.* **45**, 810-820.
- de la Torre, J. R., Goebel, B. M., Friedmann, E. I. and Pace, N. R. (2003). Microbial diversity of cryptoendolithic communities from the McMurdo Dry Valleys, Antarctica. *Appl. Environ. Microbiol.* **69**, 3858-3867.
- Deng, X., Hu, Z. A., Wang, H. X., Wen, X. G. and Kuang, T. Y. (2003). A comparison of photosynthetic apparatus of the detached leaves of the resurrection plant *Boea hygrometrica* with its non-tolerant relative *Chirita heterotrichia* in response to dehydration and rehydration. *Plant Sci.* **165**, 851-861.
- Dickie, J. B. and Prichard, H. W. (2002). Systematic and evolutionary aspects of desiccation tolerance in seeds. In *Desiccation and Survival in Plants: Drying Without Dying* (ed. M. Black and H. W. Prichard), pp. 239-259. Wallingford, UK: CAB International.
- Elbein, A. D., Pan, Y. T., Pastuszak, I. and Carroll, D. (2003). New insights on trehalose: a multifunctional molecule. *Glycobiology* **13**, 17R-27R.
- Espindola, A. D., Gomes, D. S., Panek, A. D. and Eleutherio, E. C. A. (2003). The role of glutathione in yeast dehydration tolerance. *Cryobiology* **47**, 236-241.
- Farnsworth, E. (2004). Hormones and shifting ecology throughout plant development. *Ecology* **85**, 5-15.
- Farrant, J. M. (2000). A comparison of mechanisms of desiccation tolerance among three angiosperm resurrection plant species. *Plant Ecol.* **151**, 29-39.
- Farrant, J. M., Vander Willigen, C., Loffell, D. A., Bartsch, S. and Whittaker, A. (2003). An investigation into the role of light during desiccation of three angiosperm resurrection plants. *Plant Cell Environ.* **26**, 1275-1286.
- Garay-Arroyo, A., Colmenero-Flores, J. M., Garcarrubio, A. and Covarrubias, A. A. (2000). Highly hydrophilic proteins in prokaryotes and eukaryotes are common during conditions of water deficit. *J. Biol. Chem.* **275**, 5668-5674.
- Goyal, K., Walton, L. J., Browne, J. A., Burnell, A. M. and Tunnacliffe,

- A. (2005a). Molecular anhydrobiology: identifying molecules implicated in invertebrate anhydrobiosis. *Integr. Comp. Biol.* **45**, 702-709.
- Goyal, K., Walton, L. J. and Tunnacliffe, A. (2005b). LEA proteins prevent protein aggregation due to water stress. *Biochem. J.* **388**, 151-157.
- Guidetti, R. and Jonsson, K. I. (2002). Long-term anhydrobiotic survival in semi-terrestrial micrometazoans. *J. Zool.* **257**, 181-187.
- Guo, N., Puhlev, I., Brown, D. R., Mansbridge, J. and Levine, F. (2000). Trehalose expression confers desiccation tolerance on human cells. *Nat. Biotechnol.* **18**, 168-171.
- Heideman, P. D., Rightler, M. and Sharp, K. (2005). A potential microevolutionary life-history trade-off in white-footed mice (*Peromyscus leucopus*). *Funct. Ecol.* **19**, 331-336.
- Heilmeyer, H., Durka, W., Woiitke, M. and Hartung, W. (2005). Ephemeral pools as stressful and isolated habitats for the endemic aquatic resurrection plant *Chamaegigas intrepidus*. *Phytocoenologia* **35**, 449-468.
- Heschel, M. S. and Hausmann, N. J. (2001). Population differentiation for abscisic acid responsiveness in *Impatiens capensis* (Balsaminaceae). *Int. J. Plant Sci.* **162**, 1253-1260.
- Hirai, M., Yamakawa, R., Nishio, J., Yamaji, T., Kashino, Y., Koike, H. and Satoh, K. (2004). Deactivation of photosynthetic activities is triggered by loss of a small amount of water in a desiccation-tolerant cyanobacterium, *Nostoc commune*. *Plant Cell Physiol.* **45**, 872-878.
- Hoekstra, F. A. (2002). Pollen and spores: desiccation tolerance in pollen and the spores of lower plants and fungi. In *Desiccation and Survival in Plants: Drying Without Dying* (ed. M. Black and H. W. Prichard), pp. 185-205. Wallingford, UK: CAB International.
- Hoekstra, F. A. (2005). Differential longevities in desiccated anhydrobiotic plant systems. *Integr. Comp. Biol.* **45**, 725-733.
- Hoekstra, F. A. and Golovina, E. A. (2002). The role of amphiphiles. *Comp. Biochem. Physiol.* **131A**, 527-533.
- Hoffmann, A. A., Hallas, R., Anderson, A. R. and Telonis-Scott, M. (2005). Evidence for a robust sex-specific trade-off between cold resistance and starvation resistance in *Drosophila melanogaster*. *J. Evol. Biol.* **18**, 804-810.
- Houle, G. (2002). Trade-off between growth ability and stress tolerance in *Leymus mollis* (Poaceae) along a subarctic coastal dune sequence in northern Quebec. *Can. J. Bot.* **80**, 869-874.
- Illing, N., Denby, K. J., Collett, H., Shen, A. and Farrant, J. M. (2005). The signature of seeds in resurrection plants: a molecular and physiological comparison of desiccation tolerance in seeds and vegetative tissues. *Integr. Comp. Biol.* **45**, 771-787.
- Jensen, M., Chakir, S. and Feige, G. B. (1999). Osmotic and atmospheric dehydration effects in the lichens *Hypogymnia physodes*, *Lobaria pulmonaria*, and *Peltigera aphthosa*: an *in vivo* study of the chlorophyll fluorescence induction. *Photosynthetica* **37**, 393-404.
- Jones, L. and McQueen-Mason, S. (2004). A role for expansins in dehydration and rehydration of the resurrection plant *Craterostigma plantagineum*. *FEBS Lett.* **559**, 61-65.
- Jönsson, K. I. (2005). The evolution of life histories in holo-anhydrobiotic animals: a first approach. *Integr. Comp. Biol.* **45**, 764-770.
- Jönsson, K. I. and Järemo, J. (2003). A model on the evolution of cryptobiosis. *Ann. Zool. Fenn.* **40**, 331-340.
- Kappen, L. and Valladares, F. (1999). Opportunistic growth and desiccation tolerance: the ecological success of poikilohydrous autotrophs. In *Handbook of Functional Plant Ecology* (ed. F. I. Pugnaire and F. Valladares), pp. 10-80. New York: Marcel Dekker.
- Keilin, D. (1959). The problem of anabiosis or latent life: history and current concept. *Proc. R. Soc. Lond. B Biol. Sci.* **150**, 149-191.
- Kikawada, T., Minakawa, N., Watanabe, M. and Okuda, T. (2005). Factors inducing successful anhydrobiosis in the African chironomid *Polypedium vanderplanki*: significance of the larval tubular nest. *Integr. Comp. Biol.* **45**, 710-714.
- Kranner, I. and Birtic, S. (2005). A modulating role for antioxidants in desiccation tolerance. *Integr. Comp. Biol.* **45**, 734-740.
- Li, R., Brawley, S. H. and Close, T. J. (1998). Proteins immunologically related to dehydrins in fucoid algae. *J. Phycol.* **34**, 642-650.
- Liancourt, P., Callaway, R. M. and Michalet, R. (2005). Stress tolerance and competitive-response ability determine the outcome of biotic interactions. *Ecology* **86**, 1611-1618.
- Ma, X., Jamil, K., MacRae, T. H., Clegg, J. S., Russell, J. M., Villeneuve, T. S., Euloth, M., Sun, Y., Crowe, J. H., Tablin, F. et al. (2005). A small stress protein acts synergistically with trehalose to confer desiccation tolerance on mammalian cells. *Cryobiology* **51**, 15-28.
- Mazur, P. (1968). Survival of fungi after freezing and desiccation. In *The Fungi* (ed. G. C. Ainsworth and A. L. Sussman), pp. 325-394. London: Academic Press.
- Mitchell, S. A. (1990). Factors affecting the hatching of *Streptocephalus macrourus* Daday (Crustacea; Eubranchiopoda) eggs. *Hydrobiologia* **194**, 13-22.
- Mougeot, F., Redpath, S. M., Piertney, S. B. and Hudson, P. J. (2005). Separating behavioral and physiological mechanisms in testosterone-mediated trade-offs. *Am. Nat.* **166**, 158-168.
- Murphy, D. J., Hernandez-Pinzon, I. and Patel, K. (2001). Role of lipid bodies and lipid-body proteins in seeds and other tissues. *J. Plant Physiol.* **158**, 471-478.
- Norwood, M., Toldi, O., Richter, A. and Scott, P. (2003). Investigation into the ability of roots of the poikilohydric plant *Craterostigma plantagineum* to survive dehydration stress. *J. Exp. Bot.* **54**, 2313-2321.
- Oliver, A. D., Leprince, O., Wolkers, W. F., Hinch, D. K., Heyer, A. G. and Crowe, J. H. (2001). Non-disaccharide-based mechanisms of protection during drying. *Cryobiology* **43**, 151-167.
- Oliver, A. E., Hinch, D. K. and Crowe, J. H. (2002). Looking beyond sugars: the role of amphiphilic solutes in preventing adventitious reactions in anhydrobiotes at low water contents. *Comp. Biochem. Physiol.* **131A**, 515-525.
- Oliver, M. J., Tuba, Z. and Mishler, B. D. (2000). The evolution of vegetative desiccation tolerance in land plants. *Plant Ecol.* **151**, 85-100.
- Oliver, M. J., Velten, J. and Mishler, B. (2005). Desiccation tolerance in bryophytes: a reflection of the primitive strategy for plant survival in dehydrating habitats? *Integr. Comp. Biol.* **45**, 788-799.
- Peeva, V. and Maslenkova, L. (2004). Thermoluminescence study of photosystem II activity in *Haberlea rhodopensis* and spinach leaves during desiccation. *Plant Biol.* **6**, 319-324.
- Pence, V. C. (2000). Cryopreservation of *in vitro* grown fern gametophytes. *Am. Fern J.* **90**, 16-23.
- Porembski, S. and Barthlott, W. (2000). Granitic and gneissic outcrops (inselbergs) as centers of diversity for desiccation-tolerant vascular plants. *Plant Ecol.* **151**, 19-28.
- Potts, M. (1996). The anhydrobiotic cyanobacterial cell. *Physiol. Plantarum* **97**, 788-794.
- Potts, M. (2001). Desiccation tolerance: a simple process? *Trends Microbiol.* **9**, 553-559.
- Potts, M., Slaughter, S. M., Hunneke, F.-U., Garst, J. F. and Helm, R. F. (2005). Desiccation tolerance of prokaryotes: application of principles to human cells. *Integr. Comp. Biol.* **45**, 800-809.
- Prittinen, K., Puseenius, J., Koivunoro, K. and Roininen, H. (2003). Genotypic variation in growth and resistance to insect herbivory in silver birch (*Betula pendula*) seedlings. *Oecologia* **137**, 572-577.
- Proctor, M. C. F. (2003). Comparative ecophysiological measurements on the light responses, water relations and desiccation tolerance of the filmy ferns *Hymenophyllum wilsonii* Hook. and *H. tunbrigense* (L.) Smith. *Ann. Bot.* **91**, 717-727.
- Proctor, M. C. F. and Tuba, Z. (2002). Poikilohydry and homoihydry: antithesis or spectrum of possibilities? *New Phytol.* **156**, 327-349.
- Quartacci, M. F., Glisic, O., Stevanovic, B. and Navari-Izzo, F. (2002). Plasma membrane lipids in the resurrection plant *Ramonda serbica* following dehydration and rehydration. *J. Exp. Bot.* **53**, 2159-2166.
- Rascio, N. and La Rocca, N. (2005). Resurrection plants: the puzzle of surviving extreme vegetative desiccation. *Crit. Rev. Plant Sci.* **24**, 209-225.
- Relyea, R. A. and Auld, J. R. (2005). Predator- and competitor-induced plasticity: how changes in foraging morphology affect phenotypic trade-offs. *Ecology* **86**, 1723-1729.
- Restif, O. and Koella, J. C. (2004). Concurrent evolution of resistance and tolerance to pathogens. *Am. Nat.* **164**, E90-E102.
- Ricci, C. (1998). Anhydrobiotic capabilities of bdelloid rotifers. *Hydrobiologia* **387/388**, 321-326.
- Ricci, C. and Caprioli, M. (2005). Anhydrobiosis in bdelloid species, populations, and individuals. *Integr. Comp. Biol.* **45**, 759-763.
- Ricci, C., Melone, G., Santo, N. and Caprioli, M. (2003). Morphological response of a bdelloid rotifer to desiccation. *J. Morphol.* **257**, 246-253.
- Sack, L., Grubb, P. J. and Maranon, T. (2003). The functional morphology of juvenile plants tolerant of strong summer drought in shaded forest understories in southern Spain. *Plant Ecol.* **168**, 139-163.
- Schneider, H., Wistuba, N., Wagner, H.-J., Thurmer, F. and Zimmermann, U. (2000). Water rise kinetics in refilling xylem after desiccation in a resurrection plant. *New Phytol.* **148**, 221-238.
- Sherwin, H. W. and Farrant, J. M. (1996). Differences in rehydration of three desiccation-tolerant angiosperm species. *Ann. Bot.* **78**, 703-710.

- Sherwin, H. W., Pammenter, N. W., February, E. D., Vander Willigen, C. and Farrant, J. M. (1998). Xylem hydraulic characteristics, water relations and wood anatomy of the resurrection plant *Myrothamnus flabellifolius* Welw. *Ann. Bot.* **81**, 567-575.
- Shirkey, B., Kovarcik, D. P., Wright, D. J., Wilmoth, G., Prickett, T. F., Helm, R. F., Gregory, E. M. and Potts, M. (2000). Active Fe-containing superoxide dismutase and abundant sodF mRNA in *Nostoc commune* (Cyanobacteria) after years of desiccation. *J. Bacteriol.* **182**, 189-197.
- Silvertown, J. (2004). Plant coexistence and the niche. *Trends Ecol. Evol.* **19**, 605-611.
- Sinebo, W. (2005). Trade off between yield increase and yield stability in three decades of barley breeding in a tropical highland environment. *Field Crops Res.* **92**, 35-52.
- Smith-Espinoza, C. J., Richter, A., Salamini, F. and Bartels, D. (2003). Dissecting the response to dehydration and salt (NaCl) in the resurrection plant *Craterostigma plantagineum*. *Plant Cell Environ.* **26**, 1307-1315.
- Trainor, F. R. and Gladych, R. (1995). Survival of algae in a desiccated soil: a 35-year study. *Phycologia* **34**, 191-192.
- Treonis, A. M. and Wall, D. H. (2005). Soil nematodes and desiccation survival in the extreme arid environment of the Antarctic Dry Valleys. *Integr. Comp. Biol.* **45**, 741-750.
- Tuba, Z., Lichtenthaler, H. K., Csintalan, Z., Nagy, Z. and Sente, K. (1996). Loss of chlorophylls, cessation of photosynthetic CO₂ assimilation and respiration in the poikilochlorophyllous plant *Xerophyta scabrida* during desiccation. *Physiol. Plantarum* **96**, 383-388.
- Tunnacliffe, A. and Lapinski, J. (2003). Resurrecting Van Leeuwenhoek's rotifers: a reappraisal of the role of disaccharides in anhydrobiosis. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **358**, 1755-1771.
- Tweddle, J. C., Dickie, J. B., Baskin, C. C. and Baskin, J. M. (2003). Ecological aspects of seed desiccation sensitivity. *J. Ecol.* **91**, 294-304.
- Van der Veen, I. T. (2005). Costly carotenoids: a trade-off between predation and infection risk? *J. Evol. Biol.* **18**, 992-999.
- Van Geest, G. J., Coops, H., Roijackers, R. M. M., Buijse, A. D. and Scheffer, M. (2005). Succession of aquatic vegetation driven by reduced water-level fluctuations in floodplain lakes. *J. Appl. Ecol.* **42**, 251-260.
- Vander Willigen, C., Pammenter, N. W., Mundree, S. G. and Farrant, J. M. (2004). Mechanical stabilization of desiccated vegetative tissues of the resurrection grass *Eragrostis nindensis*: does a TIP 3;1 and/or compartmentalization of subcellular components and metabolites play a role? *J. Exp. Bot.* **55**, 651-661.
- Verheyden, A., De Ridder, F., Schmitz, N., Beeckman, H. and Koedam, N. (2005). High-resolution time series of vessel density in Kenyan mangrove trees reveal a link with climate. *New Phytol.* **167**, 425-435.
- Vicre, M., Farrant, J. M. and Driouich, A. (2004a). Insights into the cellular mechanisms of desiccation tolerance among angiosperm resurrection plant species. *Plant Cell Environ.* **27**, 1329-1340.
- Vicre, M., Lerouxel, O., Farrant, J., Lerouge, P. and Driouich, A. (2004b). Composition and desiccation-induced alterations of the cell wall in the resurrection plant *Craterostigma wilmsii*. *Physiol. Plantarum* **120**, 229-239.
- Walters, C., Hill, L. M. and Wheeler, L. J. (2005). Dying while dry: kinetics and mechanisms of deterioration in desiccated organisms. *Integr. Comp. Biol.* **45**, 751-758.
- Watanabe, M., Kikawada, T., Fujita, A., Forczek, E., Adati, T. and Okuda, T. (2004). Physiological traits of invertebrates entering cryptobiosis in a post-embryonic stage. *Eur. J. Entomol.* **101**, 439-444.
- Wharton, D. A. (2003). The environmental physiology of Antarctic terrestrial nematodes: a review. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* **173**, 621-628.
- Wilson, C., Caton, T. M., Buchheim, J. A., Buchheim, M. A., Schneegurt, M. A. and Miller, R. V. (2004). DNA-repair potential of *Halomonas* spp. from the Salt Plains Microbial Observatory of Oklahoma. *Microbial Ecol.* **48**, 541-549.
- Wingler, A. (2002). The function of trehalose biosynthesis in plants. *Phytochemistry* **60**, 437-440.
- Wise, M. J. and Tunnacliffe, A. (2004). POPP the question: what do LEA proteins do? *Trends Plant Sci.* **9**, 13-17.
- Wright, J. C. (2001). Cryptobiosis 300 years on from van Leeuwenhoek: what have we learned about tardigrades? *Zool. Anz.* **240**, 563-582.
- Xie, L. T. and Klerks, P. L. (2004). Fitness cost of resistance to cadmium in the least killifish (*Heterandria formosa*). *Environ. Toxicol. Chem.* **23**, 1499-1503.
- Zeng, Y. and Kermode, A. R. (2004). A gymnosperm ABI3 gene functions in a severe abscisic acid-insensitive mutant of *Arabidopsis* (abi3-6) to restore the wild-type phenotype and demonstrates a strong synergistic effect with sugar in the inhibition of post-germinative growth. *Plant Mol. Biol.* **56**, 731-746.
- Zera, A. J. and Zhao, Z. W. (2004). Effect of a juvenile hormone analogue on lipid metabolism in a wing-polymorphic cricket: implications for the endocrine-biochemical bases of life-history trade-offs. *Physiol. Biochem. Zool.* **77**, 255-266.