The discovery, scope, and puzzle of desiccation tolerance in plants

Peter Alpert
*Department of Biology and Organismic and Evolutionary Biology and Plant Biology Graduate Programs,
University of Massachusetts, Amherst, MA 01003-5810, USA (E-mail: palpert@bio.umass.edu.)*

Abstract

The modern scientific study of desiccation tolerance began in 1702 when Anthony von Leeuwenhoek discovered that rotifers could survive without water for months. By 1860, the controversy over whether organisms could dry up without dying had reached such a pitch that a special French commission was convened to adjudicate the dispute. In 2000, we know that a few groups of animals and a wide variety of plants can tolerate desiccation in the active, adult stages of their life cycles. Among plants, this includes many lichens and bryophytes, a few ferns, and a very few flowering plants, but no gymnosperms nor trees. Some desiccation-tolerant species can survive without water for over ten years, recover from desiccation to unmeasurably low water potentials, and, when plants are desiccated, endure temperature extremes from −272 to 100 °C. Desiccation-tolerant plants occur on all continents but mainly in xeric habitats or microhabitats where the cover of desiccation-sensitive species is low. Two main puzzles arise from these patterns: What are the mechanisms by which plants tolerate desiccation? and Why are desiccation-tolerant plants not more ecologically widespread? Recent molecular and biochemical studies suggest that there are multiple mechanisms of tolerance, many of which involve protection from oxidants and from the loss of configuration of macromolecules during dehydration. Hypotheses to explain the restricted ecological range of desiccation-tolerance plants include inability to maintain a cumulative positive carbon balance during repeated cycles of wetting and drying and inherent trade offs between desiccation tolerance and growth rate.

Introduction

Desiccation tolerance can be defined as the ability of an organism to equilibrate its internal water potential with that of moderately dry air, and then resume normal function after rehydration. This requires remarkable tolerance of water deficit stress. For example, a plant that survives equilibration with 50% relative humidity must tolerate a minimum water potential of about −100 MPa and the loss of about 90% of its intracellular water (Gaff 1997).

As the term is commonly used, a 'desiccation-tolerant species' is one in which the adults tolerate desiccation, rather than just the relatively inactive stages of the life cycle such as seeds or spores. Everyday experience teaches us that this is impossible. All crops, horticultural plants, vertebrates and insects save the larvae of one desert fly (Hinton 1960) die instantly if they dry out either as adults or as juveniles. In agriculture and gardening, only seeds and spores are allowed to dry and expected to remain alive. It was therefore reasonable that the first scientific reports of desiccation tolerance in adult organisms should have been ridiculed for over a century. The first section of this paper briefly recounts the discovery and debate over the existence of desiccation tolerance, a vivid illustration of how science can amend common sense. Some plants are now known to survive extremes of drought greater than those encountered nearly anywhere on Earth. Although most of the work establishing these records is at least 25 years old, it has not recently been conveniently summarized, so a number of citations are given.

The middle section of the paper summarizes what currently appear to be the main features of the taxonomic, geographical, morphological, and ecological

scope of desiccation tolerance in plants. Desiccation tolerance in active stages of the life cycle in plants is both widespread and rare. In taxonomy, geography, and morphology, desiccation-tolerant plants are diverse but very unevenly represented among different groups, regions, and growth forms. No trees, no gymnosperms, and no North American flowering plants are known to tolerate desiccation. The ecological range of desiccation-tolerant plants is narrow. They are almost entirely restricted to places where desiccation-sensitive plants are scarce and water availability is effectively low, such as rock outcrops or the surface of larger plants. Within these habitats, desiccation-tolerant plants are often absent from the most xeric microsites, even when these microsites are completely bare of other plants.

The concluding section of the paper discusses two abiding puzzles of desiccation tolerance in plants. The first puzzle is the ability itself: What mechanisms allow some plants to survive a stress that kills the great majority of organisms? The intrinsic interest of this question, its potential applications in the development of desiccation-tolerant agricultural species, and the availability of new molecular and biochemical techniques have prompted a surge of research into the mechanism of desiccation tolerance in plants. It is clear that different species have different mechanisms, but which share common features. There have been a number of recent reviews on the mechanisms of desiccation tolerance (e.g., Leopold 1986; Crowe et al. 1992; Close et al. 1993; Smirnoff 1993; Ingram & Bartels 1996; Kranner and Grill 1997; Gaff 1997; Oliver & Bewley 1997; Farrant & Sherwin 1998), so only examples from this literature will be cited here.

The second puzzle arises from the fact that desiccation-tolerant plants seem to be at once diverse and rare. Since plants in most major groups, on all continents, and of most growth forms can tolerate desiccation, why are desiccation-tolerant plants not more abundant in productive habitats and among angiosperms? Given the exceptional extremes of drought that some desiccation-tolerant plants can withstand, why do they not at least carpet the deserts?

The discovery of desiccation tolerance

Desiccation tolerance appears to have been come to the attention of modern science during a hot spell in the summer of 1702 in Holland. Anthony von Leeuwenhoek, who had recently invented the microscope, wrote to a friend that there were microscopic animals that could survive without water (Schierbeek 1959):

> The following day the sky was very hot and dry and, about nine in the morning, I took some of the sediment which has been in the leaden gutter . . . and poured on it a small quantity of rain-water taken out of my stone cistern . . . so that if there were still any living animalcules in it they might issue forth; though I confess I never thought that there could be any living creatures in a substance so dried as this was.
>
> I was, however, mistaken; for scarce an hour had elapsed, when I saw at least a hundred of the animalcules before described.

The animals were rotifers, and van Leeuwenhoek followed his observations with a series of experiments which confirmed that rotifers could survive without water for at least five months. However, he cautiously refrained from concluding that a rotifer could survive desiccation, because he could not 'perceive that the moisture evaporated from its body'.

In the decades that followed, John Needham made a parallel discovery in England. He had been studying a disease of wheat in which the grains are replaced by inedible black galls, filled with a fibrous white pith. When he placed some of the pith in water to examine it, the fibers wriggled apart and revealed themselves to be 'eels', larvae of the plant parasitic nematode *Anguillulina tritici*. In 1743, Henry Baker reported to the Royal Society that there was no longer any doubt that living organisms could survive complete desiccation (Keilin 1959):

> 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.

Not everyone was persuaded. British, French, German, and Italian biologists conducted experiments on rotifers, nematodes, and a third group of microscopic animals, tardigrades, to support or confound the proposition that organisms could dry up without dying. The savants sometimes laced their results with invective:

> . . . indeed, based on several eyewitness testimonies . . . there exists . . . near the Orinoco a very

dangerous snake ... that can return to life, after one has left it to dry out six or twelve years, suspended from a tree branch or even in a chimney. ... Let those who believe such a story be free to believe in the resurrection of dead rotifers. (Bory Saint-Vincent, quoted in Doyère 1842)

After a century, the debate came to a head in a scientific battle between two Frenchmen. Doyère (1842) allowed tardigrades to dry in ambient air and then further desiccated them for four days in closed vessels over concentrated sulfuric acid, which reduces relative humidity to nearly 0%. Upon rehydration, the animals recovered normal activity. In Pouchet's (1859) laboratory, neither rotifers nor tardigrades recovered from drying, whether in the open air or in soil. A special commission of the Société de Biologie was appointed to settle the question. The commission reported (Broca 1860) that the rotifers in its tests had survived 82 days under vacuum followed by 30 min at 100 °C. Doyère was vindicated; Pouchet turned to an equally luckless contest with Louis Pasteur over spontaneous generation; and the controversy settled down.

Since 1860, no new groups of animals have been added to the roster of organisms that tolerate desiccation as adults. However, a prodigious ability to tolerate desiccation in the adult stage has been discovered in species of fungi and algae and many groups of plants. Some of these species can survive for many years without water. The current records for length of drought tolerated appear to be 34 years for fungi, 23 years for liverworts, 19 years for mosses, 5 years for ferns and for angiosperms, and 1 year for lichens (Table 1). A variety of desiccation-tolerant plants can survive equilibration with air of nearly 0% relative humidity, a condition achieved under vacuum or over concentrated sulfuric acid or phosphorus pentoxide. At least one fungus and a number of mosses, liverworts, ferns, fern allies, monocots, and dicots have survived such intense desiccation (Table 1; Gaff 1977).

A number of plants thus tolerate droughts that are longer and more intense than any encountered in their natural habitats. At least in bryophytes (Clausen 1952; Alpert & Oechel 1987; Davey 1997; Schipperges & Rydin 1998), relative ability to recover after droughts of different lengths is only a partial predictor of ecological range. Desiccation-sensitive species are excluded from xeric habitats, but the species that can tolerant the longest droughts are not necessarily the ones that grow in the most xeric places. This suggests either that factors other than desiccation tolerance determine the ability of these species to grow in dry sites or that length of drought tolerated is not the best measure of desiccation tolerance. One logical explanation for the evolution of tolerance of droughts longer than ever occur is that this trait is functionally linked to other traits of desiccation tolerance, and that these are the traits upon which selection is acting directly.

The ability to tolerate desiccation appears to confer or be associated with the ability to tolerate various other types of environmental stresses. Some desiccation-tolerant mosses can survive heating to 100 °C (Lange 1955; Glime & Carr 1974; Norr 1974), but they only develop such heat tolerance when dry (Meyer & Santarius 1998). Desiccation-tolerant bryophytes appear to tolerate UV-B radiation better than sensitive ones do (Takács et al. 1999). On the other hand, Wood & Gaff (1989) found no evidence that desiccation tolerance was associated with salt tolerance in the grass genus *Sporobolus*. Perhaps because freezing damage can be due largely to cell desiccation, some desiccation-tolerant species are remarkably tolerant of cold. The moss *Tortula ruralis* can recover RNA and protein synthesis after 24 hours at −198 °C (Bewley 1973). Becquerel (1951) reported that tardigrades, rotifers, the seeds of four species of plants, the spores of three species of fungi and two of bacteria, representatives of at least five genera of algae, fragments of the lichen *Xanthoria parietina,* and leaves of mosses in the genera *Grimmia and Barbula* all survived temperatures of less than 0.05 °C above absolute zero for two hours.

Becquerel had performed this test to answer a question that the discovery of desiccation tolerance had raised about the very nature of life. Can life stop, be reduced to a physical arrangement of molecules, and then restart? As Doyère (1842) put it, "Has there been a mere slowing down of the vital phenomenon ... or truly an absolute destruction which one could compare to death itself?"

It has never been agreed whether desiccation-tolerant organisms completely cease metabolism under natural conditions. On biochemical grounds (Clegg 1973), the nucleic acids and proteins in an organism with a water content of less than 0.05 g H_2O g^{-1} dry mass ought to be unable to enter into metabolic reactions. On the other hand, desiccated organisms are not completely inert. For example, when pollen of *Pinus ponderosa* is dried to a water content of less than 0.09 g H_2O g^{-1} dry mass, comparable to the water content of properly stored baking flour, the pollen still incorporates radioac-

Table 1. Records of desiccation tolerance in various plants and fungi.

Species	Desiccation treatment	Test for survival (if known)	Reference
Mosses:			
Anoectangium compactum	19 y air-dry		Malta 1921 cf. Richardson 1981
Fissidens minutifolius	6 y		Makinde 1993
Grimmia laevigata	10 y air-dry	growth	Keever 1957
Grimmia pulvinata	18-22 wk over H_2SO_4		Schröder 1886 cf. Levitt 1972
Tortula ruraliformis	14 y air-dry	production of protonemata	Bristol 1916 cf. Mueller 1972
14 species	3-7 days over P_2O_5		Hosokawa & Kubota 1957
Liverworts:			
Riccia macrocarpa	23 y air-dry	new cells at apices	Breuil-Sée 1993
two species	0% relative humidity		Abel 1956
Pteridophytes:			
Pellaea atropurpurea (prothalli and sporelings)	5 y air-dry	growth	Pickett 1931
Pellaea viridis, Cheilanthes depauperata[1]	5 y air-dry	metabolic activity[1]	Gaff 1977
Selaginella densa	2.5 y air-dry	growth and spore production	Webster & Steeves 1964
Selaginella dregei[1]	3.5 y air-dry	metabolic activity[1]	Gaff 1977
Angiosperms:			
Chamaegigas intrepidus	4 y air-dry		Hickel 1967
Xerophyta squarrosa[1]	5 y air-dry	metabolic activity[1]	Gaff 1977
Lichens:			
Ramalina maciformis	1 y at 0.01 g H_2O/g mass	normal photosynthesis	Lange 1969
Umbilicaria pustulata	> 1 y air-dry		Lange 1955
Other fungi:			
Schizophyllum commune	34 y at < 0.01 mm Hg	production of hyphae	Bisby 1945

[1] Stored as detached leaves and tested for neutral red uptake, evans blue exclusion, and chlorophyll synthesis.

tively labelled water vapor into organic compounds (Wilson et al. 1979). However, chemical reactivity is not necessarily evidence of metabolism; as Clegg (1986) pointed out: 'iron shavings consume molecular oxygen quite nicely'.

It is harder to argue with the proposition that metabolism can be completely stopped and then restarted under experimental conditions. Based on the rule of thumb that metabolic rates drop by an average of about 50% for every 10 °C decrease in temperature, Becquerel estimated that the metabolism of the organisms he cooled to near absolute zero had been slowed to less than one trillionth of normal. He reasoned that this was slow enough to be called still (Becquerel 1950): "The living matter ... of these organisms ... has become as inert as that of inanimate matter and yet it has conserved ... the property of resuming full activity".

The scope of desiccation tolerance in plants

In two major ways, the taxonomic scope of desiccation tolerance is much broader in plants than in animals. First, it appears that most plants, unlike most animals, have the capacity to tolerate desiccation in one or more of the relatively inactive stages of their life cycle, as spores, pollen, or seeds (Gaff 1980). Second, desiccation-tolerant species, those in which adults tolerate desiccation, occur in most major groups of plants but only in three of the many phyla of animals (see above). However, desiccation-tolerant species are not equally common in different plant groups (Table 2). Although species have not been systematically tested for desiccation tolerance in any group of non-flowering plants, the proportion of desiccation-tolerant species in different classes of plants probably ranges over more than two orders of magnitude, from < 0.1% in angiosperms to > 10% in mosses (Proctor 1990; Porembski 2000). Desiccation tolerance appears common though not universal

Table 2. The taxonomic distribution of desiccation tolerance in plants.

Group	Incidence
Lichens	Probably extremely common
Algae	Probably very common in terrestrial species; present in littoral species
Mosses	Probably very common
Liverworts	Probably common
Pteridophytes	Infrequent
Monocots	Rare
Dicots	Very rare (absent in N. America?)
Gymnosperms	Absent?

in bryophytes (Richardson 1981; Proctor 1990); uncommon in pteridophytes and rare in angiosperms (see references below); and absent in gymnosperms, even though gymnosperms may have desiccation-tolerant pollen or seeds (Wilson et al. 1979; Gaff 1980). Desiccation tolerance occurs in fungi, cyanobacteria, and algae (Ried 1960; Mazur 1968; Bertsch 1970; Schonbeck & Norton 1978; Dodds et al. 1995; Potts 1994, 1999) but little is known about its extent. It must be very common in lichens and in free-living algae that grow on plants, on the soil surface, or in the upper intertidal zone, since in most habitats these lichens and algae are subject to desiccation as adults.

About 330 species of vascular plants have been found to survive desiccation (Gaff 1977, 1987; Gaff & Latz 1978; Gaff & Bole 1986; Gaff & Sutaryono 1991; Porembski 2000). These include species from five families of pteridophytes (Actiniopteridaceae, Aspleniaceae, Pteridaceae, Selaginellaceae, and Sinopteridaceae), five families of monocots (Boryaceae, Cyperaceae, Poaceae, Schizaeaceae, and Velloziaceae), and three families of dicots (Gesneriaceae, Myrothamnaceae, and Scrophulariaceae) (Porembski 2000). One species in the Cactaceae (Barthlott & Porembski 1996) and *Talbotia elegans* in the Acanthaceae (Michael C. F. Proctor, personal communication) may also be desiccation-tolerant. Desiccation tolerance seems to be more common in monocots than in dicots; there are 39 known desiccation-tolerant species of grasses alone (Gaff 1997).

In different taxa, desiccation tolerance may occur as a population-, genus-, or family- level character. Perhaps most often, especially in angiosperms, a whole species will be either desiccation-tolerant or sensitive, but families with tolerant species also

have sensitive species. However, the grass species *Sporobolus fimbriatus* contains both tolerant and sensitive populations (Gaff 1986). Degree of desiccation tolerance varies between populations within species of the moss genus *Tortula* (Oliver et al. 1993), and between individuals in the dicot *Borya nitida* (Gaff 1981). At the other extreme, the family Myrothamnaceae, albeit one with only two species, is entirely desiccation-tolerant. One of the most promising avenues for future research will be further comparisons of the physiology and ecology of the conspecific populations and congeneric species that differ in ability to tolerate desiccation.

Within angiosperm taxa, populations or species may differ in the extent to which more mature parts of the plant tolerate desiccation. Species in the genus *Borya* range from ones in which only the youngest leaves recover from complete desiccation to ones in which all non-senescent leaves recover (Gaff 1989). In some grasses, only the basal meristematic zone of the leaves survives drying, while in others the whole leaf survives (Gaff & Sutaryono 1991). The floating leaves of *Chamaegigas intrepidus* lose their desiccation tolerance as they mature, whereas the floating leaves of *C. monroi*, a species from the same habitat, retain their tolerance when mature (Gaff 1986). In all these species, senescent leaves lose their ability to tolerate desiccation. This suggests that there may be a general tendency for plant cells or tissues to lose the ability to tolerate desiccation as they age.

Geographically, desiccation-tolerant vascular plants are widely but unevenly distributed. Desiccation-tolerant angiosperms occur on all continents except Antarctica but appear to be concentrated in three areas of the Southern Hemisphere: southern Africa, eastern South America, and western Australia (Gaff 1977, 1987; Gaff & Latz 1978; Porembski 2000). Different taxa predominate in each area. Individual species of desiccation-tolerant angiosperms may have small to large geographical ranges, and a few may be locally dominant; *Afrotrilepis pilosa* occurs across much of Africa, from Senegal to Gabon (Porembski et al. 1996). No desiccation-tolerant angiosperms are known from North America; in southern Europe, one (*Ramonda* [Porembski 2000]) and possibly two (*Haberlea* [Michael C. F. Proctor, personal communication]) genera in the Gesneriaceae contain desiccation-tolerant species (Porembski 2000). Desiccation-tolerant lichens and bryophytes are probably common on all continents, including Antarctica (Davey 1997).

Morphological variation in desiccation-tolerant plants shows the same three salient features as do taxonomic diversity and geographical range: breadth, unevenness, and one striking absence. Desiccation-tolerant species include caespitose, stoloniferous, and rhizomatous perennial herbs; rosette plants and woody shrubs up to 2 m tall; and probably succulents and annuals (Gaff 1986; Barthlott & Porembski 1996; Porembski 2000). They may have morphological characteristics associated with xerophytes (e.g., fibrous, needle-like leaves in *Borya nitida;* Gaff & Churchill 1976), mesophytes (broad, thin leaves in *Boea hygroscopica*; Gaff 1981), or even hydrophytes (floating leaves and aerenchyma in *Chamaegigas intrepidus*; Gaff & Geiss 1986). However, most desiccation-tolerant plants are perennial herbs and there are no known desiccation-tolerant trees. It has been suggested (e.g., Sherwin et al. 1998) that inability to reverse the cavitation of xylem may preclude desiccation-tolerant plants from growing more than a few metres tall.

The ecological range of desiccation-tolerant plants, in contrast to their broad taxonomic, biogeographical, and morphological ranges, is narrow and marginal, especially among vascular plants. Desiccation-tolerant species are found mainly in habitats that are otherwise bare of vegetation and at least occasionally subject to very low levels of water availability. For instance, Porembski (2000) estimates that nearly 90% of the known desiccation-tolerant vascular plants grow mainly on exposed rock outcrops. There seem to be true exceptions, such as desiccation-tolerant grasses that grow on relatively deep soils or in the partial shade of neighboring plants (Gaff & Sutaryono 1991). However, some apparent exceptions may be cases in which species occupy microhabitats that are bare and at times dry within habitats that are mostly vegetated and moist overall. For example, the dicot *Boea hygroscopica* grows on shaded riverbanks (Gaff 1981), but occurs in rock crevices that become seasonally dry. The microhabitats of many rock-, bark- and even soil-dwelling bryophytes and lichens are probably at times effectively dry for these plants, which equilibrate rapidly with the water potential of the surrounding air (e.g., Proctor 1990) and may experience low water availability even in wet habitats (Murray et al. 1989; Davey 1997).

Habitats in which desiccation-tolerant plants dominate the vegetation tend to be particularly arid and empty. Friedmann & Galun (1974) collected 31 desiccation-tolerant species of cyanobacteria and 12 of green algae from two arid flats in the former Soviet Union. The flats, known as takyrs, or 'places without plants' in Turkish, were 'devoid of higher vegetation and covered by a thin, brownish, elastic, somewhat lustrous, and velvety algal crust.' 'Cryptogamic crusts' consisting of desiccation-tolerant cyanobacteria, algae, often lichens, and sometimes bryophytes are widespread in desert shrublands (e.g., Johansen 1993; Lange et al. 1994). In various arid habitats, desiccation-tolerant algae (Friedmann 1971) and the moss *Aschisma kansanum* (Michael C. F. Proctor, personal communication) grow on the undersides of translucent pebbles, and tolerant lichens inhabit spaces between crystals on rocks (Friedmann 1971). Desiccation-tolerant lichens and rootless, tumbling bromeliads comprise the vegetation of some nearly rainless seashores in the Atacama Desert (Thompson & Iltis 1968; Rundel 1978). The dominant plants in small depressions on some Namibian outcrops are ecological oxymorons, desiccation-tolerant aquatic plants (Hickel 1967; Schiller et al. 1999). For example (Gaff & Giess 1986), *Chamaegigas intrepidus* (Scrophulariceae) consists of a short rhizome, thread-like adventitious roots, and two types of leaves. When a depression is filled with water, a plant bears one vertical tuft of submerged leaves about 1 cm tall and a floating, flowering rosette with four leaves each about 4 mm across. As the water evaporates, the floating leaves collapse onto the silt and all the leaves shrivel and turn purplish.

Desiccation-tolerant plants may also be excluded from the most xeric microsites in a habitat. Abundances of desiccation-tolerant bryophytes on granitic boulders at a semi-arid site in California are strongly negatively correlated with insolation (Alpert 1985); this is not due to differences in substratum or abundances of other plants. Similar patterns are reported in lichens (e.g., Kappen et al. 1980) but have apparently not been quantitatively documented in desiccation-tolerant angiosperms. Three factors that might explain this exclusion are temperature (Hearnshaw & Proctor 1982), damage by light (Gauslaa & Solhaug 1999), and carbon balance (see section on the ecology of tolerance below).

Desiccation-tolerant lichens, mosses, and bryophytes differ in their ability to make use of short periods of water availability and small amounts of water (Table 3). In general (e.g., Alpert and Oechel 1987; Csintalan et al. 1998, 1999), highly desiccation-tolerant lichens and bryophytes take < 15 min to rehydrate, < 1 h to regain net photosynthesis, and < 24 h

Table 3. Water relations in desiccation-tolerant plants: time required to dehydrate from maximum water holding capacity and to rehydrate, and ability to resume net photosynthesis after rehydration with different water sources.

	Time required to		Can rehydrate with		
	Dehydrate	Rehydrate	Rain	Dew	Water vapor
Lichens	Hours	Minutes	×	×	×[a]
Bryophytes	Hours	Minutes	×	×	
Pteridophytes	Days	Hours	×		
Angiosperms	Days	Hours	×		

[a]Lichens with green algal phycobionts.

to recover full photosynthetic function when given abundant water after a brief period of complete desiccation. Desiccation-tolerant ferns and angiosperms take 12 h to several days just to rehydrate (Gaff 1997). One exception are the diminutive aquatic species of *Craterostigma*, which can rehydrate in 1.5 h (Gaff & Giess 1986). Since lichens and bryophytes also readily absorb water through their leaves or thalli, they can rehydrate with dew (Alpert 1982; Lange et al. 1994); no desiccation-tolerant vascular plant has apparently been shown to have this ability. Lichens but apparently not bryophytes can even absorb enough water from water vapor to regain positive CO_2 uptake (Kappen et al. 1979; Rundel & Lange 1980; Hahn et al. 1993). These differences in water relations probably explain some of the differences in ecological range between groups of desiccation-tolerant plants, such as the prevalence of lichens in coastal deserts where fog is a major source of moisture (e.g., Thompson & Iltis 1968; Rundel 1978; Lange et al. 1994).

The puzzle of desiccation tolerance

The mechanisms of tolerance

It is agreed that the mechanisms of desiccation tolerance in plants lie at the cellular to subcellular levels. It is widely agreed that tolerance must include cellular mechanisms to prevent or repair two types of biochemical damage that are associated with desiccation (Table 4), oxidative damage due to the accumulation of agents such as free radicals and disruptions to ultrastructure and metabolism caused chiefly by changes in the configuration of macromolecules and disruption of membranes. Some workers (e.g., Farrant 2000) but not others (e.g., Gaff 1997) believe that mechanisms to prevent physical damage from mechanical stresses imposed by turgor loss are also important, particularly

mechanisms that prevent tearing of the plasmalemma when the cytoplasm shrinks.

In general, oxidative damage during desiccation is thought to result from metabolic imbalances, as different components of metabolism shut down at different rates. For example, one major source of oxidative damage during desiccation is probably absorption of excess light energy (Lubkeucher & Eickmeier 1991; Smirnoff 1993; Csintalan et al. 1998). Photosynthetic electron transport is often inactivated relatively early in desiccation, while light energy continues to be absorbed by photosynthetic pigments. Four of the mechanisms that may protect desiccation-tolerant plants from light energy damage as they dry (Table 4) are curling, rolling, or folding of leaves, anthocyanin synthesis, xanthophyll metabolism, and reversible loss of chlorophyll or 'poikilochlorophylly'. Desiccation-tolerant plants probably also protect themselves against oxidants by upregulating anti-oxidant activity with enzymes such as glutathione reductase and superoxidase dismutase and with other antioxidants such as carotenoids.

Macromolecules change configuration during desiccation as water becomes unavailable to interact with their hydrophilic regions (e.g., Crowe et al. 1992; Ingram & Bartels 1996). Mechanisms to stabilize the configuration of macromolecules during dehydration include the accumulation of protective proteins or non-reducing sugars (Table 4; Timasheff 1992; Crowe et al. 1998). Desiccation-tolerant angiosperms commonly hydrolyze starch as they dry (Gaff 1997), suggesting that they may be accumulating sugars. High sucrose contents may contribute to the desiccation tolerance of bryophytes (Smirnoff 1992; Marschall et al. 1998).

Desiccation damages plants as they lose water, while they remain desiccated, and when they rehydrate. Especially in species that rely on constitutive protection and repair after rehydration (see below),

Table 4. Major types of damage and some protective mechanisms implicated in desiccation tolerance.

Damage	Protective mechanism	Probable mode of action	Sample references
Oxidative damage	Leaf curling	Prevents absorption of excess light energy	Lubkeucher & Eickmeier 1991
	Anthocyanin accumulation	Absorbs excess light energy	Farrant 2000
	Xanthophyll metabolism	Dissipates excess light energy	Eickmeier et al. 1993; Deltoro et al. 1998; Beckett et al. 2000
	Poikilochlorophylly	Prevents absorption of excess light energy	Tuba et al. 1998
	Upregulation of anti-oxidant systems	Removes oxidants	Smirnoff 1993; Navari-Izzo et al. 1997
	Rapid desiccation	Minimizes time spent at intermediate water contents	Proctor 2000
Change in configuration of macromolecules, including denaturation of enzymes and loss of membrane integrity	Sugar and protein accumulation	Stabilizes molecules and membranes, 'vitrifies' cytoplasm	Muller et al. 1997; Marschall et al. 1998; Scott 2000
	Novel protein synthesis	Replaces unstable proteins	Ingram & Bartels 1996
Physical damage	Non-aqueous vacuoles	Maintains cytoplasmic volume	Farrant 2000
	Collapsible cell walls	Allows cell to shrink with cytoplasm	Vicre et al. 1999

more rapid desiccation may reduce damage during dehydration. Vascular plants that survive for months at -100 MPa may die if kept for weeks at -20 MPa (Gaff 1997), suggesting that the rate of damage during desiccation in these species is greatest at intermediate stages of dehydration. The one cactus thought to be desiccation-tolerant lacks a number of features found in other cacti that reduce water loss (Barthlott & Porembski 1996). Proctor (2000) proposes that rapid desiccation is an important mechanism by which bryophytes minimize damage during dehydration. This could explain why relatively little ultrastructural disruption is seen in some desiccation-tolerant mosses during desiccation (Oliver et al. 2000). Among seven Canary Island mosses (Hernandez-Garcia et al. 1999), species from rocks dehydrated and rehydrated more quickly than species from soil, which is likely to be less xeric. However, the degree and probability of recovery also decrease with time spent desiccated, both in vascular plants (Gaff 1977) and in bryophytes (Hinshiri & Proctor 1971; Dilks & Proctor 1974; Alpert & Oechel 1987; Davey 1997).

Clues to the genes and proteins involved in desiccation tolerance come from studies of changes in the types of gene products present as plants dehydrate and rehydrate. Proteins disappear and appear ('dehydrins') during desiccation in tolerant vascular plants (Daniel & Gaff 1980; Bartels et al. 1990; Close et al. 1993), accompanied by changes in transcription (Gaff et al. 1997). In the moss *Tortula ruralis* (Oliver et al. 2000), proteins disappear and appear ('rehydrins') during rehydration, based on translational rather than transcriptional controls. There is interesting evidence of homology between the genes associated with desiccation tolerance in the adults of some angiosperms and in both seeds (Piatkowski et al. 1990) and *Tortula ruralis* (Oliver et al. 2000). So far, no functional link has been established between individual genes and desiccation tolerance.

There is evidence that abscisic acid (ABA) acts as a signal for protective mechanisms during dehydration in both vascular plants and bryophytes (Bopp & Werner 1993; Csintalan et al. 1998; Beckett et al. 2000). However, correlation between ABA activity and desiccation tolerance is inconsistent. ABA increases as a result of low water stress in desiccation-tolerant angiosperms, but not necessarily more than in desiccation-sensitive species; adding ABA increases

desiccation tolerance in some but not all tolerant species (Gaff 1997).

It is obvious to the naked eye that mechanisms of desiccation tolerance differ between vascular species: most desiccation-tolerant monocots lose most of their chlorophyll as they desiccate and regreen after re-hydration, whereas most desiccation-tolerant dicots conserve most of their chlorophyll as they dry out (Tuba et al. 1998; Farrant 2000; Porembski 2000). Different species of the same genus may differ in this way (Gaff 1989). Interestingly, when leaves of some poikilochlorophyllous species are detached before de-hydration, the leaves remain green as they dry but they die (Gaff 1981). This suggests that chlorophyll loss is a programmed part of their desiccation toler-ance rather than a pathological consequence of drying out. All of the highly desiccation-tolerant bryophytes tested appear to conserve chlorophyll during desicca-tion (e.g., Alpert 1984; Tuba et al. 1996). Other, less visible mechanisms of desiccation tolerance also dif-fer between angiosperm species, such as the types of anti-oxidant enzymes upregulated during dehydration and changes in vacuolation or cell wall properties that counter physical stress (e.g., Vicre et al. 1999; Farrant 2000).

Oliver & Bewley (1997) hypothesize that there are fundamentally different mechanisms of desicca-tion tolerance in bryophytes and in angiosperms: bryophytes rely partly on repairs during rehydration and partly on constitutive protections, maintained dur-ing periods of full hydration; angiosperms depend largely on inducible protection mechanisms, invoked by desiccation. This may explain why rapid drying is tolerated less well by angiosperms; time is required for induction. Oliver et al. (2000) summarize the ev-idence for this hypothesis and further suggest that desiccation tolerance in the adult stage is a primitive characteristic in green plants that was lost in the evo-lution of vascular plants and then re-evolved at least once in pteridophytes and eight times in angiosperms. Not all species seem to fit the hypothesis; protone-mata of the moss *Funaria hygrometrica* appear to have 'angiosperm-like' mechanisms of tolerance.

The ecology of tolerance

Two main hypotheses have been proposed to account for the ecological rarity of desiccation-tolerant plants. One, which might be called the 'carbon balance' hy-pothesis, is that repeated cycles of wetting and drying cause desiccation-tolerance plants to suffer a cumu-lative new loss of carbon under certain regimes of water availability (Alpert & Oechel 1985; Lange et al. 1994). This hypothesis has been tested in bryophytes and lichens and could explain the inability of highly desiccation-tolerant species to colonize bare but es-pecially dry microsites (Alpert 1990). The second hypothesis, which might be called the 'productivity trade off' hypothesis, is that the ability to tolerate desiccation entails costs that constrain productivity (e.g, Oliver et al. 2000). This could make desiccation-tolerant species competitively inferior to desiccation-sensitive species in habitats where the latter can grow. This hypothesis has apparently not yet been directly tested.

Three differences between photosynthesis and res-piration favor net carbon loss by desiccation-tolerant plants during cycles of rehydration and dehydration (Kappen et al. 1979, 1980; Alpert & Oechel 1985, 1987; Proctor 1990; Lange et al. 1994; Tuba et al. 1996, 1998): photosynthesis typically requires higher water contents than respiration does; photosynthesis requires light but respiration does not; and respiration is usually elevated during recovery from desiccation. The rate of recovery of net photosynthesis is also typically slower after longer periods in the dry state (Alpert & Oechel 1987; Davey 1997). Only one dif-ference between photosynthesis and respiration seems to favor net carbon gain during a desiccation cycle: maximum gross photosynthetic rate is generally much higher than normal rates of respiration.

Whether a desiccation cycle results in a cumula-tive net gain or loss of carbon depends on the amount and timing of precipitation and insolation and on the responses of photosynthesis and respiration to water content and light. For example, Lange et al. (1994) showed that three soil lichens in the Negev Desert each respired more carbon than they assimilated over the night and morning after a light dew fall. The lichens showed a net carbon gain after a heavy dew fall. Alpert & Oechel (1985) estimated that the moss *Grimmia lae-vigata* would need to remain hydrated for about 3 h after dawn on a clear day to recoup respiratory losses of carbon after a saturating rainfall the evening before. Cover of *G. laevigata* on boulders at a chaparral site tended to be greater on north- and west-facing surfaces than on south- and east-facing surfaces, which re-ceived more direct morning sun and dried more rapidly (Alpert 1982). One way to more fully test the carbon balance hypothesis will be to model net carbon uptake as a function of water content, light, and temperature (for a recent model including water content and light,

see Williams & Flanagan 1998); and water content, light, and temperature as functions of weather and microtopography (for a relevant model of light versus microtopography, see Alpert 1985).

The 'productivity trade off' hypothesis seems plausible for at least two reasons. First, the mechanisms of desiccation tolerance could involve significant metabolic costs, both in terms of the energy they require and the energy gains they prevent. For instance, poikilochlorophylly probably requires energy for resynthesis of chlorophyll and prolongs the time between rehydration and recovery of positive net photosynthesis (Tuba et al. 1998). Second, at least in bryophytes, selection for rapid desiccation to minimize damage during desiccation should conflict with selection for traits that reduce rates of internal water loss and prolong time of hydration and thus time for growth. Traits such as close packing of shoots that increase external water holding capacity or reduce external water loss prior to internal desiccation would escape this constraint. Some species comparisons appear consistent with the productivity trade off hypothesis. Gaff (1989) observed anecdotally that the desiccation-tolerant species of grasses in one region tended to have lower rates of dry mass production than the related desiccation-sensitive species. In a comparison of two mosses, Bates (1997) reported that the more desiccation-tolerant species was less productive.

One impetus for studying desiccation tolerance in plants is that it might eventually be possible to engineer desiccation tolerance in crops and forage species (Gaff & Sutaryono 1991; Oliver & Bewley 1997). If the productivity trade off hypothesis is correct, more tolerant crops are likely to also be less productive. In ecological terms, the possibility that desiccation tolerance comes at a high price in net carbon gain may mean that the same abilities that permit desiccation-tolerant plants to colonize barren outcrops also keep them there. As succinctly phrased by Proctor (1979), desiccation tolerance may afford plants a rather cold ecological comfort:

> Bryophytes are limited by their characteristic mode of life, but also liberated; they can occupy hard substrates . . . .

References

Abel, W. O. 1956. Die Austrocknungsresistenz der Laubmoose, *Sitzungsberichte*. Osterr. Akad. Wiss. Math.-natur. Kl. Abteil. I 165 (9–10): 619–707.

Alpert, P. 1982. Poikilohydry and desiccation tolerance in some xerophytic mosses. Dissertation, Harvard University, Cambridge, Massachusetts.

Alpert, P. 1984. Analysis of chlorophyll content in mosses through extraction in DMSO. Bryologist 87: 363–365.

Alpert, P. 1985. Distribution quantified by microtopography in an assemblage of saxicolous mosses. Vegetatio 64: 131–139.

Alpert, P. 1990. Microtopography as habitat structure for mosses on rocks. Pp. 120–140. In: McCoy, E., Bell, S. A. & Mushinsky, H. (eds), Habitat structure: the physical arrangement of objects in space. Chapman and Hall, London.

Alpert, P. & Oechel, W. C. 1985. Carbon balance limits the distribution of *Grimmia laevigata*, a desiccation-tolerant plant. Ecology 66: 660–669.

Alpert, P. & Oechel, W. C. 1987. Comparative patterns of net photosynthesis in an assemblage of mosses with contrasting microdistributions. Amer. J. Bot. 74: 1787–1796.

Bartels, D., Schneider, K., Terstappen, G., Piatkowski, D. & Salamini, F. 1990. Molecular cloning of abscisic acid-modulated genes which are induced during desiccation of the resurrection plant *Craterostigma plantagineum*. Planta 181: 27–34.

Barthlott, W. & Porembski, S. 1996. Ecology and morphology of *Blossfeldia liliputana* (Cactaceae): a poikilohydric and almost astomate succulent. Bot. Acta 109: 161–166.

Barthlott, W., Gröger, A. & Porembski, S. 1993. Some remarks on the vegetation of tropical inselbergs: diversity and ecological differentiation. Biogéographica 69: 105–124.

Bates, J. W. 1997. Effects of intermittent desiccation on nutrient economy and growth of two ecologically contrasted mosses. Annal. Bot. 79: 299–309.

Beckett, R. P. 1999. Partial dehydration and ABA induce tolerance to desiccation-induced ion leakage in the moss *Atrichum androgynum*. S. Afr. J. Bot. 65: 212–217.

Beckett, R. P., Csintalan, Z. & Tuba, Z. 2000. ABA treatment increases both the desiccation tolerance of photosynthesis and non-photochemical quenching in the moss *Atrichum undulatum*. Plant Ecol. 151(1) in this issue.

Becquerel, P. 1950. La suspension de la vie des spores des bactéries et des moisissures desséchées dans le vide, vers le zéro absolue. C.R. Acad. Sci. Paris 231: 1392–1394.

Becquerel, P. 1951. La suspension de la vie des spores des algues, lichens, et mousses aux confins du zéro absolue et rôle de la synérèse réversible pour leur survie au dégel expliquant l'existence de la flore polaire et des hautes altitudes. C.R. Acad. Sci. Paris 232: 22–25.

Bertsch, A. 1970. CO_2-Gaswechsel und Wasseraushalt der aerophilen *Grünalge Apatococcus lobotus*. Planta 70: 46–72.

Bewley, J. D. 1973. Desiccation and protein synthesis in the moss *Tortula ruralis*. Can. J. Bot. 51: 203–206.

Bisby, G. R. 1945. Longevity of *Schizophyllum commune*. Nature 155: 732–733.

Bopp, M. & Werner, O. 1993. Abscisic acid and desiccation tolerance in mosses. Bot. Acta 106: 103–106.

Breuil-Sée, A. 1993. Recorded desiccation-survival times in bryophytes. J. Bryol. 17: 679–684.

Bristol, B. M. 1916. On the remarkable retention of vitality in moss protonema. New Phytol. 15: 137–143.

Broca, P. 1860. Rapport sur la question soumise à la Société de Biologie au sujet de la reviviscence des animaux desséchés. Mém. Soc. Biol., Paris 2: 1–140.

Clausen, E. 1952. Hepatics and humidity. A study on the occurrence of hepatics in a Danish tract and the influence of relative humidity on their distribution. Dansk Bot. Arkiv 15: 1–80.

Clegg, J. S. 1973. Do dried cryptobiotes have a metabolism? Pp. 141–146. In: Crowe, J. H. & Clegg, J. S. (eds), Anhydrobiosis. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pennsylvania.

Clegg, J. S. 1986. The physical properties and metabolic status of *Artemia* cysts at low water contents: the 'water replacement hypothesis'. Pp. 169–187. In: Leopold, A. C. (ed.), Membranes, metabolism, and dry organisms. Cornell University Press, New York.

Close, T. J., Fenton, R. D., Yang, A., Asghar, R., DeMason, D. A., Crone, D. E., Meyer, N. C. & Moonan, F. 1993. Dehydrin: the protein. Pp. 104–118. In: Close, T. J. & Bray, E. A. (eds), Plant responses to cellular dehydration during environmental stress. Proceedings, 16th Annual Riverside Symposium in Plant Physiology. American Society of Plant Physiologist, Rockville, Maryland.

Crowe, J. H., Clegg, J. S. & Crowe, L. M. 1998. Anhydrobiosis: the water replacement hypothesis. Pp. 440–455. In: Ried, D. S. (ed.), The properties of water in foods. Chapman & Hall, New York.

Crowe, J. H., Hoekstra, F. A. & Crowe, L. M. 1992. Anhydrobiosis. Ann. Rev. Physiol. 54: 579–599.

Csintalan, Z., Takács, Z., Proctor, M. C. F., Lichtenthaler, H. K. & Tuba, Z. 1998. Desiccation and rehydration responses of desiccation tolerant moss and lichen species from a temperate semidesert grassland. J. Hattori Bot. Club 84: 71–80.

Csintalan, Z., Proctor, M. C. F. & Tuba, Z. 1999. Chlorophyll fluorescence during drying and rehydration in the mosses *Rhytidiadelphus loreus* (Hedw.) Warnst., *Anomodon viticulosus* (Hedw.) Hook. & Tayl. and *Grimmia pulvinata* (Hedw.) Sm. Annal. Bot. 84: 235–244.

Daniel, V. & Gaff, D. F. 1980. Desiccation-induced changes in the protein complement of soluble extract from leaves of resurrection plants and related desiccation-tolerant species. Annal. Bot. 45: 163–171.

Davey, M. C. 1997. Effects of continuous and repeated dehydration on carbon fixation by bryophytes from the maritime Antarctic. Oecologia 110: 25–31.

Deltoro, V. I., Calatayud, A., Gimeno, C., Abadia, A. & Barreno, E. 1998. Changes in chlorophyll a fluorescence, photosynthetic CO_2 assimilation and xanthophyll cycle interconversions during dehydration in desiccation-tolerant and intolerant bryophytes. Planta 207: 224–228.

Dilks, T. J. K. & Proctor, M. C. F. 1974. The pattern of recovery of bryophytes after desiccation. J. Bryol. 8: 97–115.

Dodds, W. K., Gudder, D. A. & Mollenbauer, D. 1995. The ecology of *Nostoc*. J. Phycol. 31: 2–18.

Doyère, M. 1842. Sur la faculté qui possèdent les tardigrades, les rotifers, les anguillules des toits, et quelques autres animalcules, de revenir à la vie après avoir été complètement desséchées. Annal. Sci. Nat. Partie Zool. 18: 5–35.

Eickmeier, W. G., Casper, C. & Osmond, C. B. 1993. Chlorophyll fluorescence in the resurrection plant *Selaginella lepidophylla* (Hook & Grev.) Spring during high-light and desiccation stress, and evidence for zeaxanthin-associated photoprotection. Planta 189: 30–38.

Farrant, J. M. 2000. A comparison of mechanisms of desiccation tolerance among three angiosperm resurrection plant species. Plant Ecol. 151(1) in this issue.

Farrant, J. M. & Sherwin, H. W. 1998. Mechanisms of desiccation tolerance in seeds and resurrection plants. Pp. 109–120. In: Taylor, A. G. & Huang, X.-L. (eds), Progress in seed science research. Communication Services of the New York State Experimental Station, Geneva, New York.

Friedmann, L. 1971. Reflected light and scanning electron microscopy of endolithic desert algae. Phycologia 10: 411–428.

Friedmann, E. I. & Galun, M. 1974. Desert algae, lichens, and fungi. Pp. 165–212. In: Brown, G. W., Jr. (ed.) Desert biology. Academic Press, New York.

Gaff, D. F. 1977. Desiccation tolerant vascular plants of Southern Africa. Oecologia 31: 95–109.

Gaff, D. F. 1980. Protoplasmic tolerance of extreme stress. Pp. 207–230. In: Turner, N. C. & Kramer, P. J. (eds), Adaptation of plants to water and high temperature stress. John Wiley & Sons, New York.

Gaff, D. F. 1981. The biology of resurrection plants. Pp. 114–146. In: Pate, J. S. & McComb, A. J. (eds), The biology of Australian plants. University of Western Australia Press, Nedlands.

Gaff, D. F. 1986. Desiccation tolerant 'resurrection' grasses from Kenya and West Africa. Oecologia 70: 118–120.

Gaff, D. F. 1987. Desiccation tolerant plants in South America. Oecologia 74: 133–136.

Gaff, D. F. 1989. Responses of desiccation tolerant 'resurrection' plants to water stress. Pp. 255–268. In: Kreeb, K. H., Richter, H. & Hinckley, T. M. (eds), Structural and functional responses to environmental stresses. SPB Academic Publishing, The Hague, Netherlands.

Gaff, D. F. 1997. Mechanisms of desiccation tolerance in resurrection vascular plants. Pp. 43–58. In: Basra, A. S. & Basra, R. K. (eds), Mechanisms of environmental stress resistance in plants. Harwood Academic Publishers, London.

Gaff, D. F. & Bole, P. V. 1986. Resurrection grasses in India. Oecologia 71: 159–160.

Gaff, D. F. & Churchill, D. M. 1976. *Borya nitida* Labill. – an Australian species in the Liliaceae with desiccation-tolerant leaves. Aust. J. Bot. 24: 209–224.

Gaff, D. F. & Giess, W. 1986. Drought resistance in water plants in rock pools of Southern Africa. Dinteria 18: 17–37.

Gaff, D. F. & Latz, P. K. 1978. The occurrence of resurrection plants in the Australian flora. Aust. J. Bot. 26: 485–492.

Gaff, D. F. & Sutaryono, Y. A. 1991. Grasses with complete desiccation tolerance. Pp. 266–267. In: Proceedings of IVth International Rangeland Congress. French Grasslands Society, Montpellier, France.

Gaff, D. F., Bartels, D. & Gaff, J. L. 1997. Changes in gene expression during drying in a desiccation tolerant grass *Sporobolus stapfianus* and a desiccation sensitive grass *Sporobolus pyramidalis*. Aust. J. Plant Physiol. 24: 617–622.

Gauslaa, Y. & Solhaug, K. A. 1999. High-light damage in air-dry thalli of the old forest lichen *Lobaria pulmonaria* – interactions of irradiance, exposure duration and high temperature. J. Exper. Bot. 50: 697–705.

Glime, J. M. & Carr, R. E. 1974. Temperature survival of *Fontinalis novae-angliae*. Bryologist 77: 17–22.

Hahn, S. C., Tenhunen, J. D., Popp, P. W., Meyer, A. & Lange, O. L. 1993. Upland tundra in the foothills of the Brooks Range, Alaska: diurnal carbon dioxide exchange patterns of characteristic lichen species. Flora 188: 125–143.

Hearnshaw, G. F. & Proctor, M. C. F. 1982. The effect of temperature on the survival of dry bryophytes. New Phytol. 90: 221–228.

Hernandez-Garcia, C. D., Gonzales-Mancebo, J. M. & Losada-Lim, A. 1999. Water relations of some mosses growing in pine forests of Tenerife, Canary Islands. Lindbergia 24: 15–22.

Hickel, B. 1967. Contributions to the knowledge of a xerophilic water plant, *Chamaegigas intrepidus*. Int. Rev. Gesamten Hydrobiol. 53: 361–400.

Hinshiri, N. M. & Proctor, M. C. F. 1971. The effect of desiccation on subsequent assimilation and respiration of the bryophytes *Anomodon viticulosus* and *Porella platyphylla*. New Phytol. 70: 527–538.

Hinton, H. E. 1960. A fly larva that tolerates dehydration and temperatures from $-270\,°C$ to $+102\,°C$. Nature 188: 336–337.

Hosokawa, T. & Kubota, H. 1957. On the osmotic pressure and resistance to desiccation of epiphytic mosses from a beech forest, south-west Japan. J. Ecol. 45: 579–591.

Ingram, J. & Bartels, D. 1996. The molecular basis of dehydration tolerance in plants. Ann. Rev. Plant Physiol. Plant Molec. Biol. 47: 377–403.

Johansen, J. R. 1993. Cryptogamic crusts of semiarid and arid lands of North America. J. Phycol. 29: 140–147.

Kappen, L., Lange, O. L., Schulze, E.-D., Evenari, M. & Buschbom, U. 1979. Ecophysiological investigations on lichens of the Negev desert. 6. Annual course of the photosynthetic production of *Ramalina maciformis* (Del.) Bory. Flora 168: 85–108.

Kappen, L., Lange, O. L., Schulze, E.-D., Buschbom, U. & Evenari, M. 1980. Ecophysiological investigations on lichens of the Negev desert. 7. Influence of the habitat exposure on dew imbibition and photosynthetic productivity. Flora 169: 216–229.

Keever, C. 1957. Establishment of *Grimmia laevigata* on bare granite. Ecology 38: 422–429.

Keilin, D. 1959. The problem of anabiosis or latent life: history and current concept. Proc. Roy. Soc. London B 150: 149–191.

Kranner, I. & Grill, D. 1997. Desiccation and the subsequent recovery of cryptogamics that are resistant to drought. Phyton 37: 139–150.

Lange, O. L. 1955. Untersuchungen über die Hitzresistenz der Moose in Beziehung zu ihrer Verbreitung. II. Die Resistenz stark ausgetrockneter Moose. Flora 142: 381–399.

Lange, O. L. 1969. CO_2-Gaswechsel von Moosen nach Wasserdampfaufnahme aus dem Luftraum. Planta 89: 90–94.

Lange, O. L., Meyer, A., Zellner, H. & Heber, U. 1994. Photosynthesis and water relations of lichen soil crusts: field measurements in the coastal fog zone of the Namib Desert. Funct. Ecol. 8: 253–264.

Leopold, A. C. 1986. Membranes, metabolism, and dry organisms. Cornell University Press, Ithaca, New York.

Levitt, J. 1972. Responses of plants to environmental stress. Academic Press, New York.

Lubkeucher, J. G. & Eickmeier, W. G. 1991. Physiological benefits of stem curling for resurrection plants in the field. Ecology 74: 1073–1080.

Makinde, A. M. 1993. Thermotolerance of selected mosses of south-westen Nigeria savanna. Niger. J. Bot. 6: 21–25.

Malta, N. 1921. Versuche über die Widerstandsfähigkeit der Moose gegen Austrocknung. Acta Univ. Latviensis 1: 125–129.

Marschall, M., Proctor, M. C. F. & Smirnoff, N. 1998. Carbohydrate composition and invertase activity of the leafy liverwort *Porella platyphylla*. New Phytol. 138: 343–353.

Mazur, P. 1968. Survival of fungi after freezing and desiccation. Pp. 325–394. In: Ainsworth, G. C. & Sussman, A. L. (eds), The fungi. Academic Press, London.

Meyer, H. & Santarius, K. A. 1998. Short-term thermal acclimation and heat tolerance of gametophytes of mosses. Oecologia 115: 1–8.

Mueller, D. M. J. 1972. Observations on the ultrastructure of *Buxbaumia* protonema. Bryologist 75: 63–68.

Muller, J., Sprender, N., Bortlik, K., Boller, T. & Wiemken, A. 1997. Desiccation increases sucrose levels in *Ramonda* and *Haberlea*, two genera of resurrection plants in the Gesneriaceae. Physiol. Plant. 100: 153–158.

Murray, K. J., Harley, P. C., Beyers, J., Walz, H. & Tenhunen, J. D. 1989. Water content effects on photosynthetic response of *Sphagnum* mosses from the foothills of the Philip Smith Mountains, Alaska. Oecologia 79: 244–250.

Navari-Izzo, F., Quartacci, M. F. & Sgherri, C. L. M. 1997. Desiccation tolerance in higher plants related to free radical defences. Phyton-Annal. Bot. 37: 203–214.

Norr, M. 1974. Hitzresistenz bei Moosen. Flora 163: 388–397.

Oliver, M. J. & Bewley, J. D. 1997. Desiccation-tolerance of plant tissues: a mechanistic overview. Horticult. Rev. 18: 171–214.

Oliver, M. J., Mishler, B. D. & Quisenberry, J. E. 1993. Comparative measures of desiccation-tolerance in the *Tortula ruralis* complex. I. Variation in damage control and repair. Amer. J. Bot. 80: 127–136.

Oliver, M. J., Tuba, Z. & Mishler, B. D. 2000. Phylogeny of desiccation-tolerance in land plants. Plant Ecol. 151(1) in this issue..

Piatkowski, D., Schneider, K., Salamini, F. & Bartels, D. 1990. Characterization of five abscisic acid-responsive cDNA clones isolated from the desiccation tolerant plant *Craterostigma plantagineum* and their relationship to other water-stress genes. Plant Physiol. 94: 1682–1688.

Pickett, F. L. 1931. Notes on xerophytic ferns. Amer. Fern J 21: 49–56.

Porembski, S. 2000. Granitic and gneissic outcrops (inselbergs) as center of diversity for desiccation tolerant vascular plants. 151(1) in this issue.

Porembski, S., Brown, G. & Barthlott, W. 1996. A species-poor tropical sedge community: *Afrotrilepis pilosa* mats on inselbergs in West Africa. Nordic J. Bot. 16: 239–245.

Potts, M. 1994. Desiccation tolerance of prokaryotes. Microbiol. Rev. 58: 755–805.

Potts, M. 1999. Mechanisms of desiccation tolerance in cyanobacteria. Eur. J. Phycol. 57: 43–68.

Pouchet, M. 1859. Experiences sur la résistance vitale des animalcules pseudo-ressuscitants. C.R. Acad. Sci. Paris 49: 886–888.

Proctor, M. C. F. 1979. Structure and eco-physiological adaptation in bryophytes. Pp. 479–509. In: Clarke, G. C. S. & Duckett, J. G. (eds), Bryophyte systematics. Academic Press, London.

Proctor, M. C. F. 1990. The physiological basis of bryophyte production. Bot. J. Linnean Soc. 104: 61–77.

Proctor, M. C. F. 2000. The bryophyte paradox: tolerance of desiccation, evasion of drought. Plant Ecol. 151(1) in this issue.

Richardson, D. H. S. 1981. The biology of mosses. Blackwell Scientific, New York.

Ried, A. 1960. Stoffwechsel und Verbreitungsgrenzen von Flechten. II. Wasser- und Assimilationshaushalt, Entquellungs- und Submersionsresistenz von Krustenflechten benachbarter Standorte. Flora 149: 345–385.

Rundel, P. W. 1978. Ecological relationships of desert fog zone lichens. Bryologist 81: 277–293.

Rundel, P. W. & Lange, O. L. 1980. Water relations and photosynthetic response of a desert moss. Flora 169: 329–335.

Schierbeek, A. 1959. Measuring the invisible world. Abelard-Schuman Limited, London.

Schiller, P., Wolf, R. & Hartung, W. 1999. A scanning electron microscopical study of hydrated and desiccated submerged leaves of the aquatic resurrection plant *Chamaegigas intrepidus*. Flora 194: 97–102.

Schipperges, B. & Rydin, H. 1998. Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. New Phytol. 140: 677–684.

Schonbeck, M. & Norton, T. A. 1978. Factors controlling the upper limits of fucoid algaee on the shore. J. Exp. Marine. Biol. Ecol. 31: 303–313.

Schröder, G. 1886. Uber die Austrocknungsfähigkeit der Pflanzen. Dissertation, University of Tübingen, Tübingen, Germany.

Scott, P. 2000. Resurrection plants and the secrets of eternal leaf. Annal. Bot. 865: 159–166.

Sherwin, H. W., Pammenter, N. W., February, E., Vander Willigen, C. & Farrant, J. M. 1998. Xylem hydraulic characteristics, water relations and wood anatomy of the resurrection plant *Myrothamnus flabellifolius* Welw. Annal. Bot. 81: 567–575.

Smirnoff, N. 1992. The carbohydrates of bryophytes in relation to desiccation tolerance. Bryologist 17: 185–191.

Smirnoff, N. 1993. The role of active oxygen in the response of plants to water deficit and desiccation. New Phytol. 125: 27–58.

Takács, Z., Csintalan, Z., Sass, L., Laitat, E., Vass, I. & Tuba, Z. 1999. UV-B tolerance of bryophyte species with different degrees of desiccation tolerance. J. Photochem. Photobiol. B: Biol. 48: 210–215.

Timasheff, S. N. 1992. A physiochemical basis for the selection of osmolytes by nature. Pp. 70–84. In: Somero, G. N. (ed), Water and life. Springer-Verlag, New York.

Thompson, J. W. & Iltis, H. H. 1968. A fog-induced lichen community in the coastal desert of southern Peru. Bryologist 71: 31–34.

Tuba, Z., Csintalan, Z. & Proctor, M. C. F. 1996. Photosynthetic responses of a moss, *Tortula ruralis*, ssp. *ruralis*, and the lichens *Cladonia convoluta* and *C. furcata* to water deficit and short periods of desiccation, and their ecophysiological significance: a baseline study at present-day CO_2 concentration. New Phytol. 133: 353–361.

Tuba, Z., Proctor, M. C. F. & Csintalan, Z. 1998. Ecophysiological responses of homoiochlorophyllous and poikilochlorophyllous desiccation tolerant plants: a comparison and ecological perspective. Plant Growth Regul. 24: 211–217.

Vicre, M., Sherwin, H. W., Driouich, A., Jaffer, M. A. & Farrant, J. M. 1999. Cell wall characteristics and structure of hydrated and dry leaves of the resurrection plant *Craterostigma wilmsii*, a microscopical study. J. Plant Physiol. 155: 719–726.

Webster, T. R. & Steeves, T. A. 1964. Observations on drought resistance in *Selaginella densa* Rydb. Amer. Fern J 54: 189–196.

Williams, T. G. & Flanagan, L. B. 1998. Measuring and modelling environmental influences on photosynthetic gas exchange in *Sphagnum* and *Pleurozium*. Plant Cell Environ. 21: 555–564.

Wilson, A. T., Vickers, M. & Mann, L. R. B. 1979. Metabolism in dry pollen – a novel technique for studying anhydrobiosis. Naturwissenschaften 66: 53–54.

Wood, J. N. & Gaff, D. F. 1989. Salinity studies with drought resistant *Sporobolus* species. Oecologia 78: 559–564.