Chapter 16
Resurrection Plants: Physiology and Molecular Biology

Dorothea Bartels and Syed Sarfraz Hussain

Abbreviations

ABA Abscisic acid
LEA Late embryogenesis abundant
ROS Reactive oxygen species

16.1 Evolution and Geographic Distribution of Desiccation-Tolerant Plants

16.1.1 A Window into Past Research of Desiccation Tolerance

Three centuries ago science of desiccation tolerance began with a lengthy period of discovery and doubt. In 1743, Henry Baker announced to the Royal Society in London that some animals could tolerate desiccation, which means that they could dry to equilibrium with air and resume normal functions upon rehydration (Keilin 1959). Henry Baker's example of desiccation tolerance was the larva of the nematode *Anguillulina tritici*. 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, because water maintains the structure of intracellular macromolecules and membranes. The next step was to identify more organisms that tolerate desiccation. Subsequently, it was also observed in rotifers by van Leeuwenhoek in 1702 (Keilin 1959). Eventually desiccation tolerance was reported in four other phyla of animals, in some algae, fungi and bacteria, in ferns, in most bryophytes, lichens, seeds of flowering plants, and in about 300 unique angiosperm species termed resurrection plants (Alpert 2006). The vegetative tissues of resurrection plants are able to survive protoplastic dehydration of less than 2% relative water content. The majority of flowering plants and also gymnosperms have desiccation-tolerant seeds or pollen. This trait is strictly developmentally regulated, it is acquired during embryogenesis (Bartels et al. 1988) or pollen development, but lost during germination.

Among plants, desiccation tolerance is common in primitive plants such as lichens and bryophytes. This form of anhydrobiosis seems to comprise constitutively

U. Lüttge et al. (eds.), *Plant Desiccation Tolerance*, Ecological Studies 215,
DOI 10.1007/978-3-642-19106-0_16,

expressed cell protection mechanisms associated with inducible repair systems that are activated after rehydration (Oliver and Bewley 1997 and covered in detail in Chap. 4). Also among algae, it is possible to find species able to tolerate desiccation, either in terrestrial or in marine intertidal algae (Trainor and Gladych 1995; Abe et al. 2001).

The taxonomic representation of desiccation tolerance in plants is now fairly well established. Although desiccation tolerance in plants is very uncommon, it occurs in many different taxa except gymnosperms (Alpert 2000). Desiccation-tolerant species are found on all continents and among species of all growth forms except trees, but it remains a mystery why desiccation tolerance is not more widespread.

There have been only few systematic surveys for desiccation tolerance within taxa or habitats. The list of tolerant vascular plants from different regions published by Gaff and co-workers (Gaff 1977, 1986; Gaff and Latz 1978), from rock outcrops (Porembski and Barthlott 2000) and reports by Fischer (1992, 1995) (Table 16.1) are probably the closest approaches to survey higher plants (see also Tables 8.1 and 9.1). The overall pattern one sees is that taxonomic and geographic breadth is contrasted with ecological narrowness. In the 1960s, researchers started to investigate the physiological ecology of desiccation tolerance in plants, and since the 1980s, emphasis has shifted to the biochemistry and molecular biology of desiccation tolerance.

16.1.2 Evolution of Desiccation Tolerance

Many primitive autotrophs, such as cyanobacteria, are desiccation tolerant. This indicates that desiccation tolerance is a very early trait in evolution. According to Oliver et al. (2000), phylogenetic evidence exists that among land plants tolerance to vegetative desiccation was present in the basal clade of bryophytes. This adaptive trait was likely to be critical for colonization by primitive terrestrial forms of the relatively dry land environment (Kappen and Valladares 1999). With the evolution of more complex vascular plants, desiccation tolerance was lost in vegetative tissues but was retained in reproductive tissues (Oliver et al. 2000). The acquisition of desiccation tolerance is part of a maturation programme during seed development in most higher plants (Angelovici et al. 2010). The majority of terrestrial plants are capable of producing desiccation-tolerant structures such as seeds and pollen, which can remain viable in the desiccated state for long periods as demonstrated in the case of the ancient *Nelumbo nucifera* (sacred lotus) seed from China (Shen-Miller et al. 1995). It is hypothesized that desiccation tolerance was crucial for ancestral freshwater autotrophs to live on land. Independent evolution or re-evolution of desiccation tolerance has happened in the Selaginellales, leptosporangiate ferns, and in at least ten families of angiosperms. Evolutionary progress may be evident from the fact that pteridophytes, like bryophytes, are able to

Table 16.1 Desiccation-tolerant species in addition to those listed by Proctor and Pence (2002) (see also Tables 8.1 and 9.1)

Species	Country	References
Aspleniaceae		
Asplenium ceterach L. (syn.: *Ceterach officinarum*)		
Asplenium aureum and at least three further *Asplenium* species (e.g., *A. lolegnamense*) from subg. Ceterach	Canary Islands	Fischer unpublished
Gesneriaceae		
Streptocarpus: ca. 20 species (e.g., *S. bindseilii* Eb. Fisch.)	Africa	Fischer unpublished
15 Species (e.g., *S. ibityiensis* Burtt)	Madagasca	Fischer unpublished
Linderniaceae		
Craterostigma plantagineum Hochst.	Trop. Africa, Arabia, India	Fischer (1992)
Craterostigma pumilum Hochst.	East Africa, Arabia	Fischer (1992)
Craterostigma hirsutum S.Moore	East Africa	Fischer (1992)
Craterostigma purpureum Lebrun and Toussaint	Central Africa	Fischer (1992)
Craterostigma lanceolatum Skan	East Africa, Southern Afri.	Fischer (1992)
Craterostigma longicarpum Hepper	East Africa	Fischer (1992)
Craterostigma alatum Hepper	East Africa	Fischer (1992)
Craterostigma smithii S.Moore	East Africa	Fischer (1992)
Craterostigma wilmsii Diels	South Africa	Fischer (1992)
Chamaegigas intrepidus Dinter ex Heil (monotypic)	Namibia	Fischer (1992)
Lindernia acicularis Eb.Fisch.	East Africa	Fischer (1992)
Lindernia brevidens Skan	East Africa	Fischer (1992)
Lindernia abyssinica Engl.	East Africa	Fischer (1992)
Lindernia angolensis (Skan) Eb.Fisch.	Angola	Fischer (1992)
Lindernia crassifolia (Engl.) Eb.Fisch.	Angola	Fischer (1992)
Lindernia wilmsii (Engl.) Philcox	East and South Africa	Fischer (1992)
Lindernia welwitschii (Engl.) Eb.Fisch.	Angola	Fischer (1992)
Lindernia scapoidea Eb.Fisch.	Angola	Fischer (1992)
Lindernia yaundensis (S.Moore) Eb.Fisch.	Cameroon	Fischer (1992)
Lindernia niamniamensis Eb.Fisch. and Hepper	East Africa	Fischer (1992)
Lindernia philcoxii Eb.Fisch.	East Africa	Fischer (1992)
Lindernia pulchella (Skan) Philcox	East and South Africa	Fischer (1992)
Lindernia sudanica Eb.Fisch. and Hepper	East Africa	Fischer (1992)
Lindernia linearifolia (Engl.) Eb.Fisch.	Angola	Fischer (1992)
Lindernia monroi (S.Moore) Eb.Fisch.	Southern Africa	Fischer (1992)
Lindernia horombensis Eb.Fisch.	Madagascar	Fischer (1995)
Lindernia andringitrae Eb.Fisch.	Madagascar	Fischer (1995)

synthesize rehydrin proteins but can also synthesize dehydrin proteins, which are typical for angiosperms (Oliver et al. 2000).

The genes involved in desiccation tolerance were not lost, but were instead recruited for activation of drying responses in reproductive structures through inductive mechanisms during developmental programs of the plant. It seems that

resurrection plants have re-directed gene expression of seed-specific genes to be expressed in vegetative tissues (Illing et al. 2005). Recent phylogenetic evidence suggests that vascular plants gained the ability to withstand desiccation of their vegetative tissues from a mechanism present first in spore-bearing plants, and that this evolution (or re-evolution) has occurred on at least ten independent occasions within the angiosperms (Oliver et al. 2005). The presence of this information in the genomes of vascular plants permitted many species to spread over regions with seasonal rain fall and to re-evolve desiccation tolerance in vegetative tissues based on inducible responses triggered by environmental cues (Rascio and La Rocca 2005). The loss of desiccation tolerance in vegetative tissues can be interpreted as the result of suppression of genes in vegetative tissues (Dickie and Pritchard 2002). There may have been a selection against desiccation tolerance in vegetative tissues in favour of other traits. It can be concluded that the ability to survive dehydration must be basic and ubiquitous. On the other hand, desiccation tolerance must have been acquired at various advanced stages of organismic complexity by evolving metabolic or structural protective mechanisms. These must be very specific, either because of a distinct combination of quantitatively selected ubiquitous "housekeeping" mechanisms (Illing et al. 2005) or because of inventing genetic structures that act species-specific, like the *CDT-1* gene in *Craterostigma plantagineum* (Furini et al. 1997; Bartels and Salamini 2001).

16.1.3 Geographic Distribution and Ecology

Resurrection plants are found in places where rainfall is seasonal and sporadic. They often grow on rocky outcrops at low to moderate elevations in tropical and subtropical climates (Porembski and Barthlott 2000). Under these conditions, they are subjected to frequent cycles of drying and rehydration throughout the year and thus tolerate being dry in a broad range of temperatures (Mundree et al. 2002; Moore et al. 2005, 2007). Most resurrection plants have been reported from the southern hemisphere of Africa, India, Australia, and South America.

Resurrection plants have been identified within the angiosperms among both monocotyledonous and dicotyledonous plants. The dicotyledonous plants are represented mainly in the *Linderniaceae*, *Scrophulariaceae,* and *Myrothamnaceae* families, whereas the monocotyledonous are more scattered among different families. A first phylogenetic analysis among the *Scrophulariaceae* suggests a clustering of desiccation-tolerant plants represented by the genera *Craterostigma* and *Lindernia* (Rahmanzadeh et al. 2005).

It has been suggested that desiccation tolerance is connected with a size limitation, since all examples of desiccation-tolerant flowering plants do not exceed a certain height (Bewley and Krochko 1982), the largest known resurrection plant is the small woody shrub *Myrothamnus flabellifolius*, which can be between 0.5 m and 1.5 m tall (Moore et al. 2007). Most resurrection plants are herbaceous plants.

A list of desiccation-tolerant tracheophytes was compiled by Proctor and Pence (2002) and by Fischer (1992, 1995) (Table 16.1). It shows that there are more than 300 species of vascular plants. This number indicates that less than 0.15% of the total species possess vegetative desiccation tolerance.

The majority of resurrection plants were originally described in the 1970s (Gaff 1971; Gaff and Ellis 1974; Gaff and Churchill 1976; Gaff and Latz 1978). Most of the desiccation-tolerant angiosperms such as *M. flabellifolia* (Child 1960), *Xerophyta* spp., or *Craterostigma* spp. (Gaff 1977) are native to Southern Africa (especially South Africa, Namibia, and Zimbabwe) or to Australia, as it is the case for *Borya nitida* (Gaff and Churchill 1976). Physiological and anatomical characterizations of resurrection plants have been well investigated in species such as *B. nitida* (Gaff et al. 1976; Hetherington et al. 1982), *Craterostigma wilmsii* (Sherwin and Farrant 1996, 1998; Vicré et al. 1999; Cooper and Farrant 2002), *Eragrostis nindensis* (Vander Willigen et al. 2001, 2004), *M. flabellifolius* (Sherwin and Farrant 1996; Farrant and Kruger 2001), or *Reaumuria soongorica* (Liu et al. 2007) and most of the molecular aspects of desiccation tolerance have been studied in *C. plantagineum* (Bartels et al. 1990; Bartels and Salamini 2001; Hilbricht et al. 2002; Phillips et al. 2002), *Xerophyta viscosa* (Mundree et al. 2000; Mowla et al. 2002; Garwe et al. 2003) and *Xerophyta humilis* (Collett et al. 2003) and *Sporobolus* (Neale et al. 2000). A list of the most widely studied resurrection plants is compiled in Table 16.2.

Table 16.2 Best-studied resurrection plants

Name	Family	Mono/ dicot	Origin	Poikilochlorophyllous (P) Homoiochlorophyllous (H)
Xerophyta viscosa	Velloziaceae	Monocot	Southern Africa	P
Xerophyta humilis	Velloziaceae	Monocot	Southern Africa	P
Mysothamnus flabellifolia	Myrothamnaceae	Dicot	Southern Africa	H
Sporobolus stapfianus	Poaceae	Monocot	Southern Africa	
Eragrostis nindensis	Poaceae	Monocot	Southern Africa	
Craterostigma plantagineum	Scrophulariaceae	Dicot	Southern Africa	H
Craterostigma wilmsii	Scrophulariaceae	Dicot	Southern Africa	H
Lindernia brevidens	Linderniaceae	Dicot	East Africa	H
Boea hygrometrica	Gesneriaceae	Dicot	China	H
Bornetella nitida	Dasycladaceae	–	Africa, Australia, Asia	
Selaginella lepidophylla	Selaginellaceae	–	North and South America	
Tortula ruralis	Pottiacaeae	–	North America	

16.1.4 Diversity Within Linderniaceae

Phylogenetic analysis showed that desiccation-tolerant *Craterostigma* species cluster with *Lindernia* species, and the close phylogenetic relationship is supported by microsynteny between desiccation-related genes (Phillips et al. 2008). Interestingly, some members of the Linderniaceae are desiccation tolerant and some desiccation sensitive. This observation is being utilized to understand the evolution of desiccation tolerance. *Lindernia brevidens*, a close relative of *C. plantagineum*, was surprisingly identified as desiccation tolerant. This is remarkable, as *L. brevidens* is endemic to montane rainforests of East Africa, where it never experiences dry periods. *L. brevidens* occurs exclusively in two areas of the ancient Eastern Arc Mountains, which were protected from Pleistocene droughts by the mild temperatures of the Indian Ocean. High levels of species endemism and species diversity have developed in this area because of its protection and isolation. Although *L. brevidens* evolved in rainforest areas, it did not lose desiccation tolerance. Molecular analysis of desiccation-related genes suggests a high level of conservation between *L. brevidens* and *C. plantagineum* including the octulose sucrose conversion during desiccation (Phillips et al. 2008). It appears that *L. brevidens* is a neoendemic species, which has retained desiccation tolerance through genome stability. The question why *L. brevidens* did not lose desiccation tolerance cannot be answered; one hypothesis is that desiccation tolerance is linked to another trait, which is advantageous for *L brevidens* in its ecological niche. Comparative analysis between the closely related species with contrasting desiccation tolerance phenotypes could be a useful approach to understand the acquisition of desiccation tolerance.

16.2 Cellular Aspects

16.2.1 Morphological Adaptations

Leaf folding is one of the most obvious morphological changes in desiccation-tolerant vascular plants (Gaff 1989; Scott 2000; Farrant et al. 2003; Vander Willigen et al. 2003; Farrant et al. 2007). Leaves of *C. wilmsii* or *C. plantagineum*, which are fully expanded when watered, progressively curl inward during drying and become tightly folded so that only the abaxial surfaces of the older leaves in the outer whorl are exposed to the sun (Fig. 16.1 and Sherwin and Farrant 1998). Leaf folding is thought to limit oxidative stress damage from UV radiation and is thus an important morphological adaptation for surviving desiccation. Indeed, *C. wilmsii* plants do not survive desiccation in sunlight, if the leaves are mechanically prevented from folding (Farrant et al. 2003).

The leaf blades of *X. humilis* fold in half along the midrib upon dehydration, leaving only the abaxial surface exposed to the light (Sherwin and Farrant 1998).

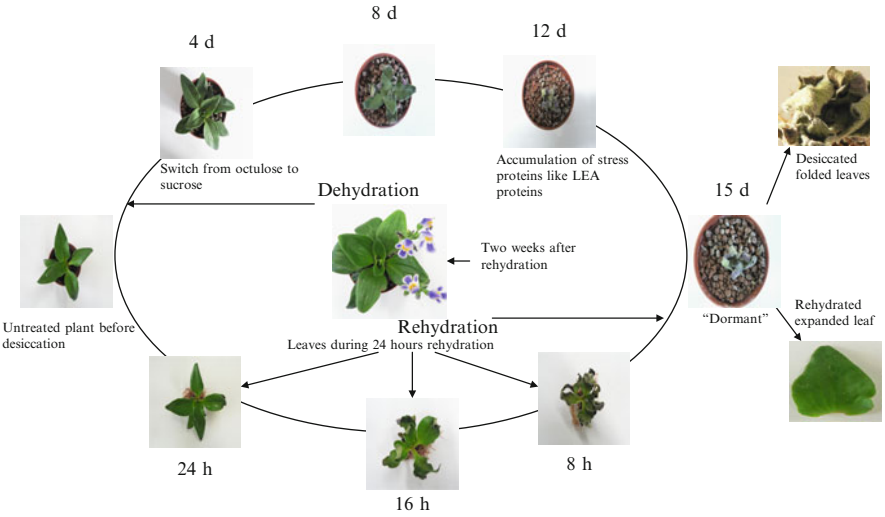

Fig. 16.1 Presentation of a dehydration and rehydration cycle in the resurrection plant *Craterostigma plantagineum*. A single plant was followed throughout the dehydration–rehydration cycle. This plant dehydrates to 2–5% RWC within 15 days and rapidly rehydrates within 24 h and starts photosynthesis. It has been estimated that leaves of this plant shrink to around 15% of the original leaf area. The plant is able to flower, as shown in the photograph in the middle; the photograph was taken 15 days after rehydration

In *Sporobulus stapfianus*, the leaf adaxial side, which is most exposed to sun radiation, is very rich in epicuticular waxes, whose function is, besides decreasing transpiration, to reflect light and to limit irradiation and temperature increase (Dalla Vecchia et al. 1998). Leaf movements occurring during dehydration have been suggested to reduce the effective transpiring surface during early stage dehydration and/or to prevent excessive irradiation of air-dry younger tissue (Gaff 1989; Farrant 2000).

16.2.2 Mechanical Stress: Cell Wall Changes, Vacuole Fragmentation and Water Substitution

One problem that resurrection plants face is the reduction of cell volume that occurs during desiccation. The examples below show that resurrection plants developed different mechanisms to avoid the potential mechanical stress during dehydration. A loss of water from cells leads to shrinkage of the central vacuole and to a drawing inward of the cell contents. This causes tension between the plasmalemma and the cell wall, which generally exhibits limited elasticity. If the cell membrane detaches

from the cell wall, plasmodesmatal connections are ruptured, which can be lethal (Cosgrove 2000). Adaptations have acquired to reduce mechanical stress. In some resurrection plants, mainly dicotyledons, the protoplast shrinkage occurring upon dehydration is accompanied by an extensive folding of cell walls, which results in a contraction of the entire cell and avoids the tearing of the plasmalemma from the cell wall (Farrant and Sherwin 1997; Thomson and Platt 1997; Farrant 2000; Vicré et al. 1999, 2004). This phenomenon prevents the development of negative turgor pressure and reduces the potential for irreversible mechanical damage (Vander Willigen et al. 2001).

Recently, a relatively high degree of cell wall flexibility was shown for *Craterostigma* and *M. flabellifolius*. This feature can be attributed to the specific composition of leaf cell walls. In *C. wilmsii*, a significant increase in xyloglucans and unesterified pectins is observed in the cell wall during drying (Vicré et al. 1999). Dehydration also induces a considerable reduction of glucose in the hemicellulose fraction of *C. wilmsii* cell walls (Vicré et al. 2004). These changes are thought to enhance the tensile strength of the cell wall, allowing it to contract and to fold without collapsing in the dried tissue. An increase in expansin activity during desiccation is associated with a rise in cell wall flexibility and folding. This increase in cell wall flexibility is correlated with an increase in expansin transcript levels and activity (Jones and McQueen-Mason 2004; Moore et al. 2008). Expansins are cell wall loosening factors and are thought to act by disrupting the hydrogen bonds between cellulose and hemicellulose polymers in the cell wall (McQueen-Mason and Cosgrove 1995). Thus, the ability of cell walls to fold by changing their chemistry and texture is an adaptive strategy of resurrection plants, but the molecular basis of this alteration is hardly known. Recently, a glycine-rich protein has been correlated with cell wall flexibility in *Boea hygrometrica* (Wang et al. 2009). These exceptional features are remarkable when compared to the rigidification of the cell wall in response to drought in non-resurrection plants (Lu and Neumann 1998; Munns et al. 2000).

Some species, especially monocotyledons, utilize a strategy of water substitution and try to maintain the original cell volume by replacing water with non-aqueous substances such as amino acids, small proteins, and sugars (Farrant 2000; Marais et al. 2004). At the same time, the central vacuole is fragmented into a number of smaller units (Quartacci et al. 1997; Dalla Vecchia et al. 1998; Vander Willigen et al. 2004). This is of advantage during desiccation, as the formation of several small vacuoles increases the surface to volume ratio and thus presents a better mechanical stability (Iljin 1957).

16.2.3 Membrane Fluidity

Membrane fluidity may be another parameter that contributes to cell and tissue flexibility during desiccation. A higher degree in polyunsaturation in membrane phospholipids results in better membrane fluidity. This was demonstrated by

changing lipid unsaturation in chloroplasts (Moon et al. 1995). Therefore, membrane composition was analysed in some resurrection plants, but the general picture is still patchy and no general conclusions can be drawn.

Hoekstra (2005) reports a negative correlation between the longevity of desiccation-tolerant tissues and the number of double bonds in the polar lipids of membranes. In desiccation-tolerant vascular plants, dehydration generally causes a decrease in total lipids as well the unsaturation level of individual phospholipids (Quartacci et al. 2002). However, the opposite trend is observed in the resurrection plant *Boea hygroscopica* where increased unsaturation of fatty acids was observed in all lipid classes upon dehydration (Navari-Izzo et al. 1995). In *S. stapfianus* phospholipid content and the level of polyunsaturated lipids within the plasma membrane increased in desiccation-tolerant, dried, attached leaves, but decreased in non-desiccation-tolerant detached leaves during desiccation (Quartacci et al. 1997; Neale et al. 2000).

16.3 Physiology

16.3.1 Photosynthesis

During desiccation, angiosperm resurrection plants shut down photosynthesis. This is correlated with down-regulation of photosynthesis-related gene expression (Bockel et al. 1998; Bernacchia et al. 1996) and with degradation of photosynthetic structures. Two different strategies are distinguished according to which plants are classified as homoiochlorophyllous and poikilochlorophyllous species (see Table 16.2). Homoiochlorophyllous species retain the chlorophyll and thylakoid membranes, although changes in photosynthetic pigment distribution are observed (Alamillo and Bartels 2001). In homoiochlorophyllous plants, chloroplasts do, however, undergo changes during desiccation, becoming roundish, with altered inner membrane organization and stacking. Also changes in the ratios between lipids and proteins as well as between the different lipid classes can occur in thylakoid membranes (Thomson and Platt 1997; Farrant 2000; Navari-Izzo et al. 2000; Quartacci et al. 1997).

In poikilochlorophyllous species, chlorophyll and the photosystem complexes are broken down (Tuba et al. 1998). The degradation of chlorophyll is advantageous, because the plants avoid the accumulation of toxic reactive oxygen species (ROS). Photosynthetic capacities are recovered during the rehydration process. Homoiochlorophyllous plants resume photosynthesis faster than poikilochlorophyllous species, which have to synthesize all components de novo. Ingle et al. (2008) demonstrated that the chloroplast biogenesis during rehydration in *X. humilis* resembles etioplast–chloroplast transition and uses similar molecular mechanisms involved in photomorphogenesis. The authors conclude from their observations that chloroplast degradation and regeneration during desiccation and rehydration do not

involve novel genes, but require altered gene regulation of genes existing probably in most higher plants.

As the photosynthetic structures in the homoiochlorophyllous species need to be protected, it is not surprising that different classes of desiccation-induced proteins seem to be involved in the maintenance of chloroplast stability (Schneider et al. 1993; Alamillo and Bartels 1996; Neale et al. 2000). One of these is a chloroplast-localized, desiccation-related protein found in the leaves of *C. plantagineum* (Bartels et al. 1992; Alamillo and Bartels 2001) and *S. stapfianus* (Neale et al. 2000) shows high similarities to early light-inducible proteins (ELIPs). The ELIPs are thylakoid chlorophyll binding proteins that are transiently expressed during greening of etiolated plants (Adamska 1997). However, they are also synthesized in mature leaves exposed to excess of light or other environmental stresses causing the enhancement of free radicals (Montané et al. 1997; Zeng et al. 2002; Provart et al. 2003; Savenstrand et al. 2004). These proteins, similar to the HLIPs (high light-induced proteins) of cyanobacteria and the LHC (light harvesting complex) proteins of photosystems, have a protective function against photo-oxidative damage of the photosynthetic apparatus (Hutin et al. 2003). ELIPs might also bind chlorophylls, thus keeping free pigments at low levels in conditions of high light stress (Hutin et al. 2003). Earlier reports suggested that ELIPs might bind zeaxanthin, taking part in the non-photochemical quenching of light energy (Król et al. 1999).

A novel nuclear gene family expressed in response to dehydration has been identified in the leaves of *C. plantagineum* (Phillips et al. 2002). The genes encode plastid-targeted proteins (CpPTP), which have the ability to interact with plastid DNA, suggesting a role in the down-regulation of chloroplast-encoded genes or a role in protecting DNA during dehydration. In addition, several classes of Lea (=late embryogenesis abundant)-like proteins and detoxifying enzymes such as aldehyde dehydrogenase were shown to accumulate in chloroplasts of *C. plantagineum* during dehydration (Schneider et al. 1993; Kirch et al. 2001).

16.3.2 Antioxidant Systems

Recovery of a resurrection plant correlates with its capacity to establish a number of antioxidant protective mechanisms during dehydration and to maintain these systems upon rehydration (Kranner et al. 2002; Kranner and Birtić 2005). The level of reactive oxgen species (ROS) undergoes a significant rise in water-stressed cells that is dictated largely by chloroplasts as they are the most aerobic compartment in plant cells (Moran et al. 1994; Kranner and Lutzoni 1999). As respiration declines early during dehydration, mitochondria may be less involved in ROS production. In conditions of water deficit, stomata close limiting the supply of CO_2 to chloroplasts. This inhibits carbon fixation and causes overexcitation of chlorophylls, which then transfer their energy to oxygen, giving rise to oxygen singlets. *M. flabellifolius* retains high concentrations of chlorophyll during desiccation. When desiccated *M. flabellifolius* was rehydrated, antioxidants such as ascorbate, glutathione, and

α-tocopherol accumulated in different tissues. When, however, the antioxidant pathways were broken down during long exposures to light, the plant did not recover anymore from desiccation (Kranner et al. 2002). This demonstrates that antioxidant systems are essential components of the recovery pathway.

In leaves of *X. viscosa*, a new desiccation-inducible antioxidant enzyme, corresponding to a form of 1-cys peroxiredoxin (Prxs), has been identified (Ndima et al. 2001; Mowla et al. 2002). Peroxiredoxins are a class of conserved thiol-specific antioxidant enzymes (Chae et al. 1994), active on substrates such as hydroperoxides, and are common to all organisms from archaebacteria to plants and mammals (Kozak 1999). The Prx found in leaves of *X. viscosa* (XvPer1) shows more than 70% sequence identity to seed-specific 1-cys peroxiredoxins (Aalen et al. 1994; Haslekas et al. 1998; Lewis et al. 2000), and it is the only 1-cys Prx that has been noticed in vegetative tissues. Its transcript is absent in fully hydrated leaves, but it accumulates upon dehydration and upon other stresses that lead to increased levels of ROS (Mowla et al. 2002). The nuclear location of XvPer1 points to an involvement of this protein in protecting the nuclear compartment from free oxygen radicals (Mowla et al. 2002).

16.3.3 Abscisic Acid Regulates Desiccation Tolerance Pathways

The plant hormone abscisic acid (ABA) is known to be involved in embryo maturation and in the response to osmotic stress in vegetative tissues. The key role of ABA was demonstrated by physiological and genetic experiments as well as measurements of ABA levels. In most resurrection plants, including the aquatic species *Chamaegigas intrepidus*, ABA is involved in attaining desiccation tolerance and in stimulating the synthesis of dehydration-induced proteins (Gaff 1980, 1989; Gaff and Loveys 1984; Bartels et al. 1990; Reynolds and Bewley 1993; Hellwege et al. 1994; Schiller et al. 1997, Chaps. 9 and 12). Leaves of *M. flabellifolia* and *B. nitida* did not survive dehydration, if they were dried so rapidly that ABA could not be accumulated (Gaff and Loveys 1984). A role for ABA in desiccation tolerance has also been demonstrated in *C. plantagineum*. Undifferentiated callus tissue of *C. plantagineum*, although intrinsically not desiccation tolerant, acquires tolerance after it has been cultured on medium containing ABA (Bartels et al. 1990). Molecular analysis suggests that ABA in resurrection plants has a similar function in signalling cascades as has ABA in dehydration responses in *Arabidopsis*. The role of ABA in signalling responses to dehydration in *Arabidopsis* has been intensively analysed through molecular genetics (Seki et al. 2007).

16.4 Gene Expression

Only a few resurrection plants have been studied on the molecular level, the best-studied species include *C. plantagineum*, *X. viscosa*, *X. humilis*, *S. stapfianus*, and *B. hygrometrica* (Table 16.2). Desiccation involves sequential gene expression

programmes. Moderate tissue dehydration creates a drought condition also requiring the activation of drought tolerance genes in resurrection plants. More substantial drying, leading to a relative water content of 3% or less, entails the utilization of additional strategies and corresponding gene expression programmes. Thus, initially general mechanisms of water-deficit responses shared with drought-tolerant species are implemented; successively, specific programmes of desiccation tolerance are activated (Neale et al. 2000). It is assumed that gene expression in resurrection plants is geared towards the synthesis of protective molecules. Desiccation-induced genes can be grouped into genes encoding regulatory factors and proteins, which may exert a protective function directly or which may represent enzymes catalysing the synthesis of other protective molecules. Examples for different groups are described below.

To investigate the molecular basis of desiccation tolerance in a vascular resurrection species, Iturriaga et al. (2006) characterized 1,046 ESTs from a cDNA library constructed from *S. lepidophylla* undergoing desiccation for 2.5 h, which represented 873 unique transcripts. Putative functions were assigned to 653 (62.4%) of these clones after comparison with protein databases, whereas 212 (20.2%) sequences having significant similarity to known sequences whose functions are unclear and 181 (17.3%) sequences having no similarity to known sequences. For those ESTs for which functional assignments were made, *S. lepidophylla* had a higher percentage of ESTs within categories of molecular chaperons, i.e., heat shock proteins or late embryogenesis abundant (LEA) proteins. Gene discovery efforts, such as EST collections, constitute an important first step in understanding which genes need to be expressed for desiccation tolerance.

16.4.1 Regulatory Molecules

In view of the fact that upon dehydration resurrection plants synthesize transcripts in vegetative tissues that are similar or even identical to the seed maturation progamme of non-tolerant plants, it seems that evolution has found a way to express genes from other pathways for desiccation tolerance in vegetative tissues. This may also be true for other stress pathways, as exemplified by a heat shock transcription factor, which is expressed in response to dehydration in *C. plantagineum* but in *Arabidopsis thaliana* only in response to high temperature (C. Bockel and D. Bartels, University of Bonn unpublished). Another example for utilizing genes of existing pathways is the formation of chloroplasts during rehydration in *X. viscosa* as discussed above. Therefore, the search for regulatory switches is important for understanding the molecular mechanisms of desiccation tolerance. However, little work on regulatory genes has been reported in resurrection plants. The largest group of characterized genes represents members of different classes of transcription factors, which seem to be very similar in sequence and in function to the corresponding counterparts from non-tolerant genetic model plants. When the transcription factors, isolated from resurrection plants, were tested in e.g., *Arabidopsis*,

they seem to function like the endogenous homlogues (for examples see below). Like it was shown for non-tolerant plants, the expression of dehydration-responsive genes in resurrection plants is mediated by ABA independent as well as ABA-dependent signal transduction pathways (Bartels 2005). It seems that the transcription factors have been optimized towards target gene activation, and it can be speculated that adaptation towards a special function in the desiccation pathway may modulate their role in gene activation. This hypothesis is in accordance with the observation that many transcription factors have been evolutionary conserved within a broad range of organisms.

Examples of the desiccation-induced transcription factors isolated thus far from resurrection plants have mainly been reported from *C. plantagineum*. Many of them belong to the Myb, the homeodomain-leucine zipper (HD-Zip), or the bZip (basic leucine zipper) families (Iturriaga et al. 1996; Frank et al. 1998; Ditzer and Bartels 2006). Plant myb-related genes comprise a large family and are likely to participate in a variety of functions (Meissner et al. 1999). Two Myb-related genes, *cpm10* and *cpm7*, show differential expression and regulation in response to desiccation and ABA in *C. plantagineum* (Iturriaga et al. 1996). *Cpm10* is expressed in undifferentiated callus tissue and is up-regulated by ABA, while *cpm7* is induced by dehydration in roots. Transgenic *Arabidopsis* plants overexpressing *cpm10* displayed increased tolerance to drought and salt stress (Villalobos et al. 2004). These plants also showed ABA hypersensitivity and glucose insensitivity, suggesting that *cpm10* is involved in mediating ABA and glucose signalling responses in *Arabidopsis* as well as in the response to drought stress. HD-ZIP genes encode proteins that have only been identified in plants so far and are thought to regulate development and responses to environmental cues (Ramanjulu and Bartels 2002). Two HD-Zip genes, CPHB-1 and CPHB-2, are induced by dehydration in leaves and roots of *C. plantagineum*, but show different responses to exogenously applied ABA (Frank et al. 1998). ABA treatment induces the transcription of CPHB-2, but not that of CPHB-1. Five other HD-Zip genes have been isolated from *C. plantagineum*, two of which were induced by ABA in undifferentiated callus, while the other three were not. This suggests that these HD-Zip genes act in different pathways of the dehydration response; some mediated by ABA, while others are independent of ABA (Deng et al. 2002).

Research related to dehydration- and cold-regulated genes in *Arabidopsis* led to the discovery of the dehydration-responsive elements (DRE) (Yamaguchi-Shinozaki and Shinozaki 1993). Therefore, many genes that are responsive to cold and drought stress contain DRE/CRT (dehydration-responsive element/C-repeat) elements within their 5′ regulatory regions and are regulated by DREB/CBF (DRE-binding protein/C-repeat binding factor) transcription factors (Stockinger et al. 1997; Liu et al. 1998). The DREB/CBF proteins belong to the AP2/EREBP (ethylene-responsive element binding protein) family of transcription factors which are important regulators of flower development and plant responses to abiotic stresses (Riechmann and Meyerowitz 1998; Shigyo et al. 2006). One such AP2/EREBP transcription factor has been reported as a regulator of the drought response pathway in *S. stapfianus* (Le 2005).

Other characterized genes that are involved in the regulatory network are phospholipases, VP1 homologues, or the SAP domain transcription factor CpR18 (Bartels et al. 2006). Like for the nature of the regulatory genes, the recognition promoter elements seem to be conserved, and no desiccation-specific elements have been identified so far (Bartels et al. 2006). This supports the hypothesis that no new mechanisms were invented, but that new combinations of regulatory elements are sufficient for expressing genes in desiccation tolerance.

Mutants would be extremely valuable for the unravelling of the basis of desiccation tolerance, but no genetic system has been developed yet to generate mutants in resurrection plants. The reason for this is that most resurrection plants appear not to be diploid. Over 10 years ago an activation tagging approach, which generates dominant mutations led to the discovery of the unusual *CDT-1* gene in *C. plantagineum* (Furini et al. 1997). No homologues of this gene have so far been identified in species apart from *Craterostigma*. Constitutive overexpression of *cdt-1* leads to desiccation tolerance in *C. plantagineum* callus tissue activating the expression of desiccation-induced transcripts. *CDT-1* transcripts accumulate in response to desiccation, but no corresponding polypeptides are synthesized; thus, *CDT-1* functions as a regulatory, non-protein coding RNA (Hilbricht et al. 2008 (see also Chap. 13.3)). *CDT-1* is a member of a large gene family, of which all members have features of retrotransposons (Smith-Espinoza et al. 2005). Retrotransposon elements may be required for expression of desiccation tolerance, as they are able to activate genes via small RNAs such as CDT-1. Small RNAs as regulators of gene expression are emerging players for essential environmental and developmental switches (Phillips et al. 2007).

16.4.2 Aquaporins

Aquaporin-mediated water transport across membranes provides a fundamental contribution to plant–water relations (Maurel and Chrispeels 2001 and Chap. 10). This makes it obvious to assume that aquaporins are involved in desiccation tolerance. In leaves of *C. plantagineum*, one TIP (tonoplast intrinsic protein) and several PIP (plasma membrane intrinsic protein) have been found, whose genes are differentially expressed during dehydration (Mariaux et al. 1998). A dehydration-responsive TIP has also been isolated from leaves of *S. stapfianus* (Neale et al. 2000). One particularly relevant finding is the identification of a tonoplast aquaporin, namely TIP 3;1, in dried leaves of *E. nindensis* (Vander Willigen et al. 2004). The interest in this desiccation-dependent channel protein is due to the fact that a TIP 3;1 had never been noticed in vegetative tissues. TIP 3;1 proteins (formerly called α-TIPs) are considered to be unique to orthodox seeds (Maurel et al. 1995). It participates in modulating the water permeability of the tonoplast during rehydration and may aid in mobilizing sugars, proteins, and other solutes that have accumulated inside the small vacuoles of bundle sheath cells with which it is associated (Vander Willigen et al. 2004).

16.4.3 Carbohydrates

A common observation in the desiccation process is the accumulation of soluble sugars, and the importance of sugars has been implicated in several studies. During desiccation, starch is rapidly converted into glucose (Crowe et al. 1998). Apart from a role in osmotic adjustment during the dehydration phase, the protective effects of sugars may also include protein stabilization in desiccated cells (Ramanjulu and Bartels 2002). Conversion of starch into sucrose is attributed primarily through activation of sucrose phosphate synthase by reversible protein phosphorylation upon perception of osmotic stress. Sucrose and trehalose have been proposed to prevent protein denaturation and membrane fusions (Crowe et al. 1998; Peters et al. 2007). Both sugars are capable of forming biological glasses (a process called vitrification) within the dried cell. Vitrification of the cytoplasm may not be due to the effects of sugars only, but probably results from the interaction of sugars with other molecules, most likely proteins (Hoekstra 2005). Cells of many desiccation-tolerant plants and animals undergo vitrification upon drying to protect organelles from damage (Buitink and Leprince 2004), and conformational changes of proteins and membrane fusion are prevented (Crowe et al. 1998). Vitrification is thought to limit the production of free radicals by slowing down chemical reactions and molecular diffusion in the cytoplasm (Hoekstra 2005). Thus, vitrification may be an important protective mechanism for resurrection plants.

In fully hydrated *S. stapfianus*, leaves, glucose, fructose, and galactose are present in large amounts. During dehydration, sucrose increases to high levels in air-dry leaves to become the predominant sugar (Ghasempour et al. 1998). Other sugars such as raffinose and trehalose are also detected, and they may complement the role of sucrose as osmotic protectants during drying (Rascio and La Rocca 2005). The changes in sugar composition observed in *S. stapfianus* leaves were quantitatively similar to those reported for other resurrection plants where the common trend was the conversion of monosaccharides in hydrated leaves into sucrose in dried leaves and vice versa in rehydrated leaves (Murelli et al. 1996). In *C. plantagineum*, the unusual eight-carbon sugar, 2-octulose, is the predominant sugar in hydrated leaves, which is converted to sucrose, with the reverse process being observed during rehydration (Bianchi et al. 1991). Sucrose also accumulates in the roots of drying *C. plantagineum*, although the most prevalent sugar stachyose does not undergo big changes (Bianchi et al. 1991; Norwood et al. 2003).

Sugar conversions during the desiccation process have been correlated with corresponding gene expression. Again, it seems that no new genes have evolved, but the conversion processes utilize existing genes of the sugar metabolism. Sucrose biosynthetic genes have been shown to be induced by both desiccation and ABA in the resurrection plant *C. plantagineum* (Kleines et al. 1999). Perhaps gene duplications may happen during acquisition of desiccation tolerance to accommodate desiccation-related metabolism. A possible example for this is the presence of a transketolase localized in the cytoplasm of *C. plantagineum*. It has been suggested that this transketolase is involved in the octulose sucrose conversions

during the dehydration/rehydration cycle and has changed its substrate specificity (Willige et al. 2009).

16.4.4 Compatible Solutes

A common phenomenon in drought stress is the accumulation of organic compatible solutes because they are supposed to stabilize proteins and membranes (Levitt 1980; Crowe and Crowe 1992). Upon dehydration, many plants accumulate non-toxic solutes such as proline, mannitol, and glycine betaine (Chen and Murata 2002). The compatible solute accumulation results in an increase in cellular osmolarity, which in turn leads to an influx of water into, or at least a reduced efflux from cells (Hare et al. 1998). The main function of compatible solutes is, however, not so much to increase the water holding capacity of cells, but compatible solutes have been proposed to protect cells through the stabilization of cytoplasmic constituents and ion sequestration (Hare et al. 1998). This is due to the preferential exclusion of these compounds from the surfaces of proteins and membranes, which thus remain preferentially hydrated (Hoekstra et al. 2001).

Several resurrection plants have been analysed for the presence of potential compatible solutes. A diverse spectrum of molecules, which may serve as compatible solutes, has been identified, but no general mechanism is identified. Inositol, present in *X. viscosa*, may be an effective osmoprotectant (Mayee et al. 2005). Application of proline had no effect on detached leaves of *B. nitida* and *M. flabellifolius* (Gaff 1980). In the latter species, polyphenols have been identified that might be relevant to desiccation tolerance, as provenances from Namibia subjected to greater drought stress were genetically different from those in South Africa and contained more and different polyphenols (e.g., 3,4,5-tri-*O*-galloquinic acid) (Moore et al. 2005). *M. flabellifolius* contains a broad spectrum of potential osmotica in particular glucose–glycerol, which has been directly correlated with osmotic tolerance in cyanobacteria (Bianchi et al. 1993).

16.4.5 Protective Proteins: LEA Proteins and Heat Shock Proteins

The abundant accumulation of proteins during desiccation is the most obvious change on the molecular level. The majority of the proteins are LEA proteins. LEA proteins accumulate during seed maturation and during dehydration of vegetative tissues. A protective role for the LEA proteins has been suggested, and it is assumed that they are a major contribution to desiccation tolerance in resurrection plants (Ingram and Bartels 1996; Mtwisha et al. 2006). Despite this fact LEA proteins are not discussed further in this chapter, as there have been excellent recent reviews discussing LEA proteins in detail (Battaglia et al. 2008; Tunnacliffe and Wise 2007 and references within). Besides LEA proteins also heat shock

proteins are associated with desiccation. The role of heat shock proteins in this context is summarized.

Proteins commonly indicated as heat shock proteins, being up-regulated by heat stress, also seem to be implicated in desiccation tolerance (Goyal et al. 2005). They are induced by the same stresses as LEA proteins and their synthesis coincides with the acquisition of desiccation tolerance (Wehmeyer et al. 1996; Mtwisha et al. 2006). These proteins function as molecular chaperones and play primary roles in protein biosynthesis, folding, assembly, intracellular localization, secretion, and degradation of other proteins (Feder and Hofmann 1999). Intracellular proteins such as heat shock proteins can compensate the loss of hydrogen bonds to water molecules by hydrogen's bonding to other molecules. Generally, HSPs are able to maintain partner proteins in a folding competent, folded or unfolded, state to minimize the aggregation of non-native proteins or to target non-native or aggregated proteins for degradation or removal from the cell (Feder and Hofmann 1999). This function could be important in maintaining cells in resurrection plants viable.

Small heat shock proteins are expressed in the vegetative tissue of *C. plantagineum* during water stress and are correlated with desiccation-tolerant callus (Alamillo et al. 1995) and in the cysts of the desiccation-tolerant brine shrimp *Artemia franciscana* under desiccation stress (Clegg 2005).

16.5 Rehydration

Most research on resurrection plants has examined strategies that counteract desiccation damage and promote survival in the dry state. Less attention has been paid to the rehydration process. The events occurring during rehydration involve gradual recovery of correct cellular organization, which is accompanied by reactivation of normal metabolic functions. The processes leading to the reestablishment of vital functions and metabolic activities are an integral part of the entire phenomenon of desiccation tolerance. It seems that there are differences in the rehydration process in lower plants such as mosses and in higher vascular plants. It has been discussed whether desiccation tolerance in mosses such as *Tortula ruralis* is constitutive, with recovery essentially a matter of reassembly of components conserved intact through a drying–rehydration cycle, or non-constitutive repair processes. The idea of a repair-based mechanism of desiccation tolerance in bryophytes was introduced by Bewley (Bewley 1979; Bewley and Krochko 1982). It was extended by Oliver and Bewley (1984) to take into account the fine-structural change, and it has since been reiterated in a succession of reviews (Bewley and Oliver 1992; Oliver 1996; Oliver and Bewley 1997; Oliver et al. 1998).

The successful rehydration in *C. plantagineum* requires a discrete period of time (Bartels et al. 1990). Dried *Craterostigma* plants complete the water uptake in 12–15 h when placed in a water-saturated environment. The comparison of protein patterns from dried and rehydrated leaves of *C. plantagineum* revealed that no new mRNAs were detectable during early phases of rehydration

(Bernacchia et al. 1996). Within the first 6–12 h of rewatering, desiccation-related transcripts and their corresponding proteins disappear. Only after 12–15 h, when the leaf tissues reach about 80–90% RWC, changes occur in translatable mRNA populations and protein profiles, mainly related to enhanced expression of genes that were down-regulated upon drying. New photosynthetic pigments are synthesized, and respiration, photosynthesis and other metabolic pathways are reactivated, showing that mRNAs or enzymes necessary to restore cell activities had been accumulated in a stable form during dehydration and were sufficiently protected in the dry state.

Even though the desiccation tolerance of resurrection plants largely depends on strategies of cell protection during drying, these plants also have mechanisms for preventing and/or repairing cell damage upon rehydration (Cooper and Farrant 2002). In rehydrated leaves of several species, the de novo synthesis of some proteins, also produced upon drying, has been observed. Proteins involved in both dehydration and rehydration include the previously mentioned expansins (Cooper and Farrant 2002). Moreover, aquaporins, whose mRNAs are produced and stored during the late stage of drying, also seem to play an important role in rehydration by regulating the rate of water flow into cells (Mariaux et al. 1998).

16.6 Conclusions and Outlook

In this chapter, we have tried to summarize what is known about the physiology and molecular analysis of desiccation tolerance in higher plants. The phenomenon of desiccation tolerance has been well characterized for a few species. However, the mechanism is not understood yet. The obstacles are the complexity of desiccation tolerance and the lack of genetic approaches connected with the complex genomes. The genomes known so far are relatively small in estimated size, but they are not diploid. Recently, DNA sequencing technologies have become available at an economically affordable level. This will allow transcriptome analysis for plant species for which no genome sequence is available and thus a comparative genomic analysis could provide more insight into desiccation tolerance (Rodriguez et al. 2010). It can be expected from such approaches to identify genes that are unique to desiccation-tolerant species and thus could give a clue for the requirements of desiccation tolerance.

In addition to understanding which genes are expressed and which proteins are active, epigenetic mechanisms turn out to be a new dimension of modifying adaptations to responses to environmental stresses. This has not been studied at all in any resurrection plants but needs to be considered for explaining desiccation tolerance mechanisms. Epigenetic mechanisms can be seen as enhancing the complexity of regulation of gene expression and may enhance the flexibility of plant genomes to adapt to diverse environments.

Acknowledgements We thank Prof. E. Fischer for advice on the geographical distribution of desiccation-tolerant species and for providing the information contained in Table 16.1. Work in the laboratory of D.B. was supported by grants from the German Research Council, by the European training network ADONIS and by an ERA-PG project. D.B. is a member of the European COST action INPAS (International Network of Plant Abiotic Stress). We thank C. Marikar for help with the manuscript preparation.

References

Aalen RB, Opsahl-Ferstad HG, Linnestad C, Olsen OA (1994) Transcripts encoding an oleosin and a dormancy-related protein are present in both the aleurone layer and the embryo of developing barley (*Hordeum vulgare* L.) seeds. Plant J 5:385–396

Abe S, Kurashima A, Yokohama Y, Tanaka J (2001) The cellular ability of desiccation tolerance in Japanese intertidal seaweeds. Bot Mar 44:125–131

Adamska I (1997) ELIPs. Light-induced stress proteins. Physiol Plant 100:794–805

Alamillo JM, Bartels D (1996) Light and stage of development influence the expression of desiccation-induced genes in the resurrection plant *Craterostigma plantagineum*. Plant Cell Environ 19:300–310

Alamillo JM, Bartels D (2001) Effects of desiccation on photosynthesis pigments and the ELIP-like dsp 22 protein complexes in the resurrection plant *Craterostigma plantagineum*. Plant Sci 160:1161–1170

Alamillo J, Roncarati R, Heino P, Velasco R, Nelson D, Elster R, Brenacchia G, Furini A, Schwall G, Salamini F, Bartels D (1995) Molecular analysis of desiccation tolerance in barley embryos and in the resurrection plant *Craterostigma plantagineum*. Agronomie 2:161–167

Alpert P (2000) The discovery, scope, and puzzle of desiccation tolerance in plants. Plant Ecol 151:5–17

Alpert P (2006) Constraints of tolerance: why are desiccation-tolerant organisms so small and rare. J Exp Biol 209:1575–1584

Angelovici R, Galili G, Fernie AR, Fait A (2010) Seed desiccation: a bridge between maturation and germination. Trends Plant Sci 15(4):211–218

Bartels D (2005) Desiccation tolerance studied in the resurrection plant *Craterostigma plantagineum*. Integr Comp Biol 45:696–701

Bartels D, 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

Bartels D, Singh M, Salamini F (1988) Onset of desiccation tolerance during development of the barley embryo. Planta 175:485–492

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

Bartels D, Hanke C, Schneider K, Michel D, Salamini F (1992) A desiccation-related ELIP-like gene from the resurrection plant *Craterostigma plantagineum* is regulated by light and ABA. EMBO J 11:2771–2778

Bartels D, Ditzer A, Furini A (2006) What can we learn from resurrection plants? In: Ribaut JM (ed) Drought adaptation in cereals. New York, Hayworth, pp 599–622

Battaglia M, Olvera-Carrillo Y, Garciarrubio A, Campos F, Covarrubias AA (2008) The enigmatic LEA proteins and other hydrophilins. Plant Physiol 148:6–24

Bernacchia G, Salamini F, Bartels D (1996) Molecular characterization of the rehydration process in the resurrection plant *Craterostigma plantagineum*. Plant Physiol 111:1043–1050

Bewley JD (1979) Physiological aspects of desiccation tolerance. Ann Rev Plant Physiol 30:195–238

Bewley JD, Krochko JE (1982) Desiccation tolerance. In: Pirson A, Zimmermann MH (eds) Encyclopedia of plant physiology, vol 12b, New series. Springer, Heidelberg, pp 325–378

Bewley JD, Oliver MJ (1992) Desiccation-tolerance in vegetative plant tissues and seeds: protein synthesis in relation to desiccation and a potential role for protection and repair mechanisms. In: Osmond CB, Somero G (eds) Water and life: a comparative analysis of water relationship at the organismic, cellular and molecular levels. Springer, Berlin, pp 141–160

Bianchi G, Gamba A, Murelli C, Salamini F, Bartels D (1991) Novel carbohydrate metabolism in the resurrection plant *Craterostigma plantagineum*. Plant J 1(3):355–359

Bianchi G, Gamba A, Limiroli R, Pozzi N, Elste R, Salamini F, Bartels D (1993) The unusual sugar composition in leaves of the resurrection plant *Myrothamnus flabellifolia*. Physiol Plant 87:223–226

Bockel C, Salamini F, Bartels D (1998) Isolation and characterization of genes expressed during early events of the dehydration process in the resurrection plant *Craterostigma plantagineum*. J Plant Physiol 152:158–166

Buitink J, Leprince O (2004) Glass formation in plant anhydrobiotes: survival in the dry state. Cryobiology 48:215–228

Chae HZ, Chung SJ, Rhee SG (1994) Thioredoxin-dependent peroxide reductase from yeast. J Biol Chem 269:27670–27678

Chen THH, Murata N (2002) Enhancement of tolerance of abiotic stress by metabolic engineering of betaines and other compatible solutes. Curr Opin Plant Biol 5:250–257

Child GF (1960) Brief notes on the ecology of the resurrection plant *Myrothamnus flabellifolia* with mention of its water-absorbing abilities. J S Afr Bot 26:1–8

Clegg JS (2005) Desiccation tolerance in encysted embryos of the animal extremophile, *Artemia*. Integr Comp Biol 45:715–724

Collett H, Butowt R, Smith J, Farrant JM, Illing N (2003) Photosynthetic genes are differentially transcripted during the dehydration-rehydration cycle in the resurrection plant, *Xerophyta humilis*. J Exp Bot 54:2593–2595

Cooper K, Farrant JM (2002) Recovery of the resurrection plant *Craterostigma wilmsii* from desiccation: protection versus repair. J Exp Bot 53:1805–1813

Cosgrove DJ (2000) Expansive growth of plant cell walls. Plant Physiol Biochem 38:109–124

Crowe JH, Crowe LM (1992) Membrane integrity in anhydrobiotic organisms: towards a mechanism for stabilizing dry cells. In: Somero GN, Osmond CB, Bolin CL (eds) Water and life. A comparative analysis of water relationships at the organismic, cellular and molecular levels. Springer, Berlin, pp 87–113

Crowe JH, Carpenter JF, Crowe LM (1998) The role of vitrification in anhydrobiosis. Annu Rev Plant Physiol 60:73–103

Dalla Vecchia F, Asmar TE, Calamassi R, Rascio N, Vazzana C (1998) Morphological and ultrastructural aspects of dehydration and rehydration in leaves of *Sporobolus stapfianus*. Plant Growth Reg 24:219–228

Deng X, Phillips J, Meijer AH, Salamini F, Bartels D (2002) Characterization of five novel dehydrationresponsive homeodomain leucine zipper genes from the resurrection plant *Craterostigma plantagineum*. Plant Mol Biol 49:601–610

Dickie JB, Pritchard HW (2002) Systematic and evolutionary aspects of desiccation tolerance in seeds. In: Black M, Pritchard HW (eds) Desiccation and survival of plants – drying without dying. CABI, Wallingford, pp 239–259

Ditzer A, Bartels D (2006) Identification of stress-responsive promoter elements and isolation of corresponding DNA binding proteins for the LEA gene *CpC2* promoter. Plant Mol Biol 61:643–663

Farrant JM (2000) A comparation of mechanisms of desiccation tolerance among three angiosperm resurrection plant species. Plant Ecol 151:29–39

Farrant JM, Kruger LA (2001) Longevity of dry *Myrothamnus flabellifolius* in simulated field conditions. Plant Growth Reg 35:109–120
Farrant JM, Sherwin HW (1997) Mechanisms of desiccation tolerance in seeds and resurrection plants. In: Taylor AG, Huang XL (eds) Progress in seed research. Proceedings of the second international conference on seed science and technology. Communication Services of the New York State Agricultural Experimental Station, Geneva, NY, pp 109–120
Farrant JM, Vander Willigen C, Loffell DA, Bartsch S, Whittaker A (2003) An investigation into the role of light during desiccation of three angiosperm resurrection plants. Plant Cell Environ 26:1275–1286
Farrant JM, Brandt W, Lindsey GG (2007) An overview of mechanisms of desiccation tolerance in selected angiosperm resurrection plants. Plant Stress 1(1):72–84
Feder ME, Hofmann GE (1999) Heat shock proteins, evolutionary and ecological physiology. Ann Rev Physiol 61:243–282
Fischer E (1992) Systematik der afrikanischen Lindernieae (Scrophulariaceae). Tropische und subtropische Pflanzenwelt 81:1–365
Fischer E (1995) Revision of the Lindernieae (Scrophulariaceae) in Madagascar. 1. The genera *Lindernia* Allioni and *Crepidorhopalon* E. FISCHER. Bull Mus Natl Hist Nat Paris 4e sér., 17, section B, Adansonia: 227–257
Frank W, Phillips JR, Salamini F, Bartels D (1998) Two dehydration-inducible transcripts from the resurrection plant *Craterostigma plantagineum* encode interacting homeodomain-leucine zipper proteins. Plant J 15:413–421
Furini A, Koncz C, Salamini F, Bartels D (1997) High level transcription of a member of a repeated gene family confers dehydration tolerance to callus tissue of *Craterostigma plantagineum*. EMBO J16:3599–3608
Gaff DF (1971) Desiccation-tolerant flowering plants in southern Africa. Science 174:1033–1034
Gaff DF (1977) Desiccation tolerant vascular plants of southern Africa. Oecologia 31:95–109
Gaff DF (1980) Protoplasmic tolerance of extreme water stress. In: Turner NC, Kramer PJ (eds) Adaptation of plants to water and high temperature stress. Wiley, New York, pp 207–230
Gaff DF (1986) Desiccation tolerant "resurrection" grasses from Kenya and West Africa. Oecologia 70:118–120
Gaff DF (1989) Responses of desiccation-tolerant "resurrection" plants to water stress. SPB Academic, The Hague
Gaff DF, Churchill DM (1976) *Borya nitida* Labill. – an Australian species in the Liliaceae with desiccation-tolerant leaves. Aust J Bot 24:209–224
Gaff DF, Ellis RP (1974) Southern African grasses with foliage that revives after dehydration. Bothalia 11:305–308
Gaff DF, Latz PK (1978) The occurrence of resurrection plants in the Australian flora. Aust J Bot 26:485–492
Gaff DF, Loveys BR (1984) Abscisic-acid content and effects during dehydration of detached leaves of desiccation tolerant plants. J Exp Bot 35:1350–1358
Gaff DF, Zee S-Y, O'Brien TP (1976) The fine structure of dehydrated and reviving leaves of *Borya nitida* Labill. – a desiccation-tolerant plant. Aust J Bot 24:225–236
Garwe D, Thomson JA, Mundree SG (2003) Molecular characterization of XVSAP1, a stress-responsive gene from the resurrection plant *Xerophyta viscosa* Baker. J Exp Bot 54:191–201
Ghasempour HR, Gaff DF, Williams RPW, Gianello RD (1998) Contents of sugars in leaves of drying desiccation-tolerant flowering plants, particularly grasses. Plant Growth Reg 24:185–191
Goyal K, Walton LJ, Tunnacliffe A (2005) LEA proteins prevent protein aggregation due to water stress. Biochem J 388:151–157
Hare PD, Cress WA, Van Staden J (1998) Dissecting the role of osmolyte accumulation during stress. Plant Cell Environ 21:535–553
Haslekas C, Stacy RAP, Nygaard V, Culianez-Macia FA, Aalen RB (1998) The expression of a peroxiredoxin antioxidant gene, AtPer1, in *Arabidopsis thaliana* is seed-specific and related to dormancy. Plant Mol Biol 36:833–845

Hellwege EM, Dietz KJ, Volk OH, Hartung W (1994) Abscisic acid and the induction of desiccation tolerance in the extremely xerophilic liverwort *Exormotheca holstii*. Planta 194:525–531

Hetherington SE, Smillie RM, Hallam ND (1982) Humidity-sensitive degreening and regreening of leaves of *Borya nitida* Labill. as followed by changes in chlorophyll fluorescence. Aust J Plant Physiol 9:587–599

Hilbricht T, Salamini F, Bartels D (2002) CpR18, a novel SAP-domain plant transcription factor, binds to a promoter region necessary for ABA mediated expression of the CdeT27–45 gene from the resurrection plant *Craterostigma plantagineum* Hochst. Plant J 31:293–303

Hilbricht T, Varotto S, Sgaramella V, Bartels D, Salamini F, Furini A (2008) Retrotransposons and siRNA have a role in the evolution of desiccation tolerance leading to resurrection of the plant *Craterostigma plantagineum*. New Phytol 179:877–887

Hoekstra FA (2005) Differential longevities in desiccated anhydrobiotic plant systems. Integr Comp Biol 45:725–733

Hoekstra FA, Golovina EA, Buitink J (2001) Mechanisms of plant desiccation-tolerance. Trends Plant Sci 6:431–438

Hutin C, Nussaume L, Moise N, Moya I, Kloppstech K, Havaux M (2003) Early light-induced proteins protect Arabidopsis from photooxidative stress. Proc Natl Acad Sci USA 100:4921–4926

Iljin WS (1957) Drought-resistance in plants and physiological processes. Annu Rev Plant Physiol 3:341–363

Illing N, Denby KJ, Collett H, Shen A, Farrant JM (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

Ingle RA, Collett H, Cooper K, Takahashi Y, Farrant JM, Illing N (2008) Chloroplast biogenesis during rehydration of the resurrection plant *Xerophyta humilis*: parallels to the etioplast-chloroplast transition. Plant Cell Environ 31:1813–1824

Ingram J, Bartels D (1996) The molecular basis of dehydration-tolerance in plants. Annu Rev Plant Physiol Plant Mol Biol 47:377–403

Iturriaga G, Leyns L, Villegas A, Gharaibeh R, Salamini F, Bartels D (1996) A family of novel myb-related genes from the resurrection plant *Craterostigma plantagineum* are specifically expressed in callus and roots in response to ABA or desiccation. Plant Mol Biol 32:707–716

Iturriaga G, Cushman MAF, Cushman JC (2006) An EST catalogue from the resurrection plant *Selaginella lepidophylla* reveals abiotic stress-adaptive genes. Plant Sci 170:1173–1184

Jones L, McQueen-Mason S (2004) A role for expansins in dehydration and rehydration of the resurrection plant *Craterostigma plantagineum*. FEBS Lett 559:61–65

Kappen L, Valladares F (1999) Opportunistic growth and desiccation tolerance: the ecological success of poikilohydrous autotrophs. In: Pugnaire FI, Valladares F (eds) Handbook of functional plant ecology. Marcel Dekker, New York, pp 10–80

Keilin D (1959) The problem of anabiosis or latent life: history and current concept. Proc R Soc Lond B Biol Sci 150:149–191

Kirch HH, Nair A, Bartels D (2001) Novel ABA- and dehydration-inducible aldehyde dehydrogenase genes isolated from the resurrection plant *Craterostigma plantagineum* and *Arabidopsis thaliana*. Plant J 28(5):555–567

Kleines M, Elster RC, Rodrigo MJ, Blervacq AS, Salamini F, Bartels D (1999) Isolation and expression analysis of two stress-responsive sucrose-synthase genes from the resurrection plant *Craterostigma plantagineum* (Hochst.). Planta 209:13–24

Kozak CA (1999) Genetic mapping of six mouse peroxiredoxin genes and fourteen peroxiredoxin related sequences. Mamm Genome 10:1017–1019

Kranner I, Birtić S (2005) A modulating role for antioxidants in desiccation tolerance. Integr Comp Biol 45:734–740

Kranner I, Lutzoni F (1999) Evolutionary consequences of transition to a lichen symbiotic state and physiological adaptation to oxidative damage associated with poikilohydry. In: Lerner HR (ed) Plant responses to environmental stress. From phytohormones to genome reorganization. Marcel Dekker, New York, pp 591–628

Kranner I, Beckett RP, Wornik S, Zorn M, Pfeinhofer W (2002) Revival of a resurrection plant correlates with its antioxidant status. Plant J 31:13–24

Król M, Ivanov MG, Jansson S, Kloppstech K, Huner NPA (1999) Greening under high light or cold temperature affects the level of xanthophyllcycle pigments, early light-inducible proteins, and light-harvesting polypeptides in wild-type barley and the chlorina f2 mutant. Plant Physiol 120:193–203

Le TN (2005) Genetics of desiccation tolerance in the resurrection plant *Sporobolus stapfianus*. PhD thesis. Monash University, Melbourne, Australia

Levitt J (1980) Responses of plants to environmental stresses, vol 2, Water, radiation, salt and other stresses. Academic, New York

Lewis ML, Miki K, Veda T (2000) FePer1, a gene encoding an evolutionary conserved 1-Cys peroxiredoxin in buckwheat (*Fagopyrum esculentum* Moench), is expressed in a seed-specific manner and induced during seed germination. Gene 246:81–91

Liu Q, Kasuga M, Sakuma Y, Abe H, Miura S, Yamaguchi-Shinozaki K, Shinozaki K (1998) Two transcription factors, DREB1 and DREB2, with an EREBP/AP2 DNA binding domain separate two cellular signal transduction pathways in drought and low temperature responsive gene expression, respectively, in Arabidopsis. Plant Cell 10:1391–1406

Lu ZJ, Neumann PM (1998) Water stressed maize, barley and rice seedlings show species diversity in mechanisms of leaf growth inhibition. J Exp Bot 49:1945–1952

Liu Y, Tengguo Z, Li X, Wang J (2007) Protective mechanisms of desiccation tolerance in *Reaumuria soongorica*. Sci China Ser C-Life Sci 50:15–21

Marais S, Thomson JA, Farrant JM, Mundree SG (2004) X_V VHA-C"-1 a novel stress responsive V-ATPhase Subnit C" homologue isolated from the resurrection plant *Xerophyta viscos*a. Plant Physiol 122:54–64

Mariaux JB, Bockel C, Salamini F, Bartels D (1998) Desiccationand abscisic acid-responsive genes encoding major intrinsic proteins (MIP) from the resurrection plant *Craterostigma plantagineum*. Plant Mol Biol 38:1089–1099

Maurel C, Chrispeels MJ (2001) Aquaporins. A Molecular entry into plant water relations. Plant Physiol 125:135–138

Maurel C, Kado RT, Guern J, Chrispeels MJ (1995) Phosphorylation regulates the water channel activity of the seed-specific aquaporin α-TIP. EMBO J 14:3028–3035

Mayee MB, Mundree SG, Majumder AL (2005) Molecular cloning, bacterial overexpression and characterization of L-myo-inositol 1-Phosphate Synthase from a monocotyledonous resurrection plant, *Xerophyta viscosa*. J Plant Biochem Biotechnol 14:95–98

McQueen-Mason SJ, Cosgrove DJ (1995) Expansin mode of action on cell walls – analysis of wall hydrolysis, stress-relaxation, and binding. Plant Physiol 107:87–100

Meissner RC, Jin H, Cominelli E, Denekamp M, Fuertes A, Greco R, Kranz HD, Penfield S, Petronik K, Urzainqui A, Martin C, Paz-Ares J, Smeekens S, Tonelli C, Weisshaar B, Baumann E, Klimyuk V, Marillonnet S, Patel S, Speulman E, Tissier AF, Bouchez D, Jones JDG, Periera A, Wisman E, Bevan M (1999) Function search in a large transcription factor gene family in Arabidopsis assessing the potential of reverse genetics to identify insertional mutations in R2R3 MYB genes. Plant Cell 11:1827–1840

Montané MH, Dreyer S, Triantaphylides C, Kloppstech K (1997) Early light-inducible proteins during long-term acclimation of barley to photooxidative stress caused by light and cold: high level of accumulation by posttranscriptional regulation. Planta 202:293–302

Moon BY, Higashi S, Gombos Z, Murata N (1995) Unsaturation of the membrane lipids of chloroplasts stabilizes the photosynthetic machinery against low-temperature photoinhibition in transgenic tobacco plants. Proc Natl Acad Sci USA 92(14):6219–6223

Moore JP, Lindsey FJM, GG BWF (2005) The South African and Namibian populations of the resurrection plant *Myrothamnus flabellifolius* are genetically distinct and display variation in their galloquinic acid composition. J Chem Ecol 31:2823–2834

Moore JP, Lindsey GG, Farrant JM, Brandt WG (2007) An overview of the biology of desiccation tolerant resurrection plant *Myrothamnus flabellifolia*. Ann Bot 99:211–217

Moore JP, Vicré-Gibouin M, Farrant JM, Driouich A (2008) Adaptations of higher plant cell walls to water loss: drought vs desiccation. Physiol Plant 134:237–245

Moran JF, Becana M, Iturbe-Ormaetxe I, Frechilla S, Klucas RV, Aparecio-Tejo P (1994) Drought induces oxidative stress in pea plants. Planta 194:346–352

Mowla SB, Thomson JA, Farrant JM, Mundree SG (2002) A novel stress-inducible antioxidant enzyme identified from the resurrection plant *Xerophyta viscosa* Baker. Planta 215:716–726

Mtwisha L, Farrant J, Brandt W, Lindsey GG (2006) Protection mechanisms against water deficit stress: desiccation tolerance in seeds as a study case. In: Ribaut J (ed) Drought adaptation in cereals. Haworth, New York, pp 531–549

Mundree SG, Whittaker A, Thomson JA, Farrant JM (2000) An aldose reductase homolog from the resurrection plant *Xerophyta viscose* Baker. Planta 211:693–700

Mundree SG, Baker B, Mowla S, Peters S, Marais S, Vander Willigen C, Govender K, Maredza A, Muyanga S, Farrant JM, Thomson JA (2002) Physiological and molecular insights into drought tolerance. Afr J Biotechnol 1:28–38

Munns R, Passioura JB, Guo JM, Chazen O, Cramer GR (2000) Water relations and leaf expansion: importance of time scale. J Exp Bot 51:1495–1504

Murelli C, Adamo V, Finzi PV, Albini FM, Bochicchio A, Picco AM (1996) Sugar biotransformations by fungi on leaves of the resurrection plant *Sporobolus stapfianus*. Phytochemistry 43:741–745

Navari-Izzo F, Ricci F, Vazzana C, Quartacci MF (1995) Unusual composition of thylakoid membranes of the resurrection plant Boea hygroscopica: changes in lipids upon dehydration and rehydration. Physiol Plant 94:135–142

Navari-Izzo F, Quartacci MF, Pinzino C, Rascio N, Vazzana C, Sgherri C (2000) Protein dynamics in thylakoids of the desiccation-tolerant plant Boea hygroscopica during dehydration and rehydration. Plant Physiol 124:1427–1436

Ndima T, Farrant JM, Thomson J, Mundree S (2001) Molecular characterization of XVT8, a stress-responsive gene from the resurrection plant *Xerophyta viscosa* Baket. Plant Growth Reg 35:137–145

Neale AD, Blomstedt CK, Bronson P, Le TN, Guthridge K, Evand D, Gaff DF, Hamill JD (2000) The isolation of genes from the resurrection grass *Sporobolus stapfianus* which are induced during severe drought stress. Plant Cell Environ 23:265–277

Norwood M, Toldi O, Richter A, 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 MJ (1996) Desiccation-tolerance in vegetative plant cells. Physiol Plant 97:779–787

Oliver MJ, Bewley JD (1984) Desiccation and ultrastructure in bryophytes. Adv Bryology 2:91–131

Oliver MJ, Bewley JD (1997) Desiccation-tolerance in plant tissues. A mechanistic overview. Hortic Rev 18:171–214

Oliver MJ, Wood AJ, O'Mahony P (1998) "To dryness and beyond" – preparation for the dried state and rehydration in vegetative desiccation tolerant plants. Plant Growth Reg 24:193–201

Oliver MJ, Tuba Z, Mishler BD (2000) The evolution of vegetative desiccation tolerance in land plants. Plant Ecol 151:85–100

Oliver MJ, Velten J, Mishler BD (2005) Desiccation tolerance in bryophytes: a reflection of the primitive strategy for plant survival in dehydrating habitats? Integr Comp Biol 45:788–799

Peters S, Mundree SG, Thomson JA, Farrant JM, Keller F (2007) Protection mechanisms in the resurrection plant *Xerophyta viscosa* (Baker): both sucrose and raffinose family oligosaccharides (RFOs) accumulate in leaves in response to water deficit. J Exp Bot 58(8):1947–1956

Phillips JR, Hilbricht T, Salamini F, Bartels D (2002) A novel abscisic acid- and dehydration-responsive gene family from the resurrection plant *Craterostigma plantagineum* encodes a plastid-targeted protein with DNA binding activity. Planta 215:258–266

Phillips JR, Dalmay T, Bartels D (2007) The role of small RNAs in abiotic stress. FEBS Lett 581:3592–3597

Phillips JR, Fischer E, Baron M, van den Dries N, Facchinelli F, Kutzer M, Rahmanzadeh R, Remus D, Bartels D (2008) Lindernia brevidens: a novel desiccation-tolerant vascular plant, endemic to ancient tropical rainforests. Plant J 54:938–948

Porembski S, Barthlott W (2000) Granitic and gneissic outcrops (inselbergs) as centers of diversity for desiccation-tolerant vascular plants. Plant Ecol 151:19–28

Proctor MCF, Pence VC (2002) Vegetative tissues: bryophytes, vascular resurrection plants, and vegetative propogules. In: Black M, Pritchard HW (eds) Desiccation and survival in plants: drying without dying. CABI, Wallingford, Oxon, pp 207–237

Provart NJ, Gil P, Chen W, Han B, Chang HS, Wang X, Zhu T (2003) Gene expression phenotypes of Arabidopsis associated with sensitivity to low temperatures. Plant Physiol 132:893–906

Quartacci MF, Forli M, Rascio N, DallaVecchia F, Bochicchio A, Navari-Izzo F (1997) Desiccation-tolerant *Sporobolus stapfianus*: lipid composition and cellular ultrastructure during dehydration and rehydration. J Exp Bot 48:1269–1279

Quartacci MF, Glisic O, Stevanovic B, Navari-Izzo F (2002) Plasma membrane lipids in the resurrection plant *Ramonda serbica* following dehydration and rehydration. J Exp Bot 53:2159–2166

Rahmanzadeh R, Müller K, Fischer E, Bartels D, Borsch T (2005) The Linderniaceae and Gratiolaceae are further lineages distinct from the Scrophulariaceae (Lamiales). Plant Biol 7:1–12

Ramanjulu S, Bartels D (2002) Drought- and desiccation-induced modulation of gene expression in plants. Plant Cell Environ 25:141–151

Rascio N, La Rocca N (2005) Resurrection plants: the puzzle of surviving extreme vegetative desiccation. Crit Rev Plant Sci 24:209–225

Reynolds TL, Bewley JD (1993) Abasicic acid enhances the ability of the desiccation tolerant fern *Polypodium virginianum* to withstand drying. J Exp Bot 44:1771–1779

Riechmann JL, Meyerowitz EM (1998) The AP2/EREBP family of plant transcription factors. Biol Chem 379:633–646

Rodriguez M, Edsgard D, Hussain SS, Alquezar A, Rasmussen M, Gilbert T, Nielsen B, Bartels D, Mundy J (2010) Transcriptomes of the desiccation tolerant resurrection plant *Craterostigma plantagineum*. Plant J 63:212–228

Savenstrand H, Olofsson M, Samuelsson M, Strid A (2004) Induction of early-inducible protein gene expression in *Pisum sativum* after exposure to low levels of UV-B radiation and other environmental stresses. Plant Cell Rep 22:532–536

Schiller P, Heilmeier H, Hartung W (1997) Absisic acid (ABA) relations in the aquatic resurrection plant *Chamaegigas intrepidus* under naturally fluctuating environmental conditions. New Phytol 136:603–611

Schneider K, Wells B, Schmelzer E, Salamini F, Bartels D (1993) Desiccation leads to the rapid accumulation of both cytosol and chloroplast proteins in the resurrection plant *Craterostigma plantagineum* Hochst. Planta 189:120–131

Scott P (2000) Resurrection plants and the secrets of eternal leaf. Ann Bot 85:159–166

Seki M, Umezawa T, Urano K, Shinozaki K (2007) Regulatory metabolic networks in drought stress responses. Curr Opin Plant Biol 10:296–302

Shen-Miller J, Mudgett MB, Schopf JW, Clarke S, Berger R (1995) Exceptional seed longevity and robust growth – ancient sacred lotus from China. Am J Bot 82:1367–1380

Sherwin HW, Farrant JM (1996) Differences in rehydration of three desiccation tolerant angiosperm species. Ann Bot 78:703–710

Sherwin HW, Farrant JM (1998) Protection mechanisms against excess light in the resurrection plants *Craterostigma wilmsii* and *Xerophyta viscosa*. Plant Growth Reg 24:203–210

Shigyo M, Haseba M, Ito M (2006) Molecular evolution of the AP2 subfamily. Gene 366:256–265

Smith-Espinoza CJ, Phillips JR, Salamini F, Bartels D (2005) Identification of further *Craterostigma plantagineum* cdt mutants affected in abscisic acid mediated desiccation tolerance. Mol Gen Genom 274:364–372

Stockinger EJ, Gilmour SJ, Thomashow MF (1997) Arabidopsis thaliana CBF1 encodes an AP2 domain-containing transcriptional activator that binds to the C-repeat/DRE, a cisacting DNA

regulatory element that stimulates transcription in response to low temperature and water deficit. Proc Natl Acad Sci USA 94:1035–1040

Thomson WW, Platt KA (1997) Conservation of cell order in desiccated mesophyll of *Selaginella lepidophylla* ([Hook and Grev.] Spring). Ann Bot 79:439–447

Trainor FR, Gladych R (1995) Survival of algae in a desiccated soil: a 35-year study. Phycologia 34:191–192

Tuba Z, Proctor MCF, Csintalan Z (1998) Ecophysiological responses of homoiochlorophyllous and poikilochlorophyllous desiccation-tolerant plants: a comparison and an ecological perspective. Plant Growth Reg 24:211–217

Tunnacliffe A, Wise MJ (2007) The continuing conundrum of the LEA proteins. Naturwissenschaften 94:791–812

Vander Willigen C, Farrant JM, Pammenter NW (2001) Anomalous pressure volume curves of resurrection plants do not suggest negative turgor. Ann Bot 88:537–543

Vander Willigen C, Pammenter CNW, Jaffer MA, Mundree SG, Farrant JM (2003) An ultrastructural study using anhydrous fixation of *Eragrostis nindensis*, a resurrection grass with both desiccation-tolerant and sensitice tissues. Funct Plant Biol 30:1–10

Vander Willigen C, Pammenter NW, Mundree SG, Farrant JM (2004) Mechanical stabilization of desiccated vegetative tissues of the resurrection grass *Eragrostis nindensis*: does a TIP 3;1 and/or compartimentation of subcellular components and metabolites play a role? J Exp Bot 397:651–661

Vicré M, Sherwin HW, Driouich A, Jaffer MA, Farrant JM (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

Vicré M, Lerouxel O, Farrant J, Lerouge P, Driouich A (2004) Composition and desiccation-induced alterations of the cell wall in the resurrection plant *Craterostigma wilmsii*. Physiol Plant 120:229–239

Villalobos MA, Bartels D, Iturriaga G (2004) Stress tolerance and glucose insensitive phenotypes in Arabidopsis overexpressing the CpMYB10 transcription factor gene. Plant Physiol 135:309–324

Wang L, Shang H, Liu X, Wu R, Zheng M, Phillips J, Bartels D, Deng X (2009) A cell wall localised glycine-rich protein plays a role in dehydration tolerance in the resurrection plant *Boea hygrometrica*. Plant Biol 12:1–13

Wehmeyer N, Hernandez LD, Finkelstein RR, Vierling E (1996) Synthesis of small heat shock proteins is part of the developmental program of late seed maturation. Plant Physiol 112:747–757

Willige B, Kutzer M, Tebartz F, Bartels D (2009) Subcellular localization and enzymatic properties of differentially expressed transketolase genes isolated from the desiccation tolerant resurrection plant *Craterostigma plantagineum*. Planta 229:659–666

Yamaguchi-Shinozaki K, Shinozaki K (1993) The plant hormone abscisic acid mediates the drought-induced expression but not the seed-specific expression of rd22, a gene responsive to dehydration stress in *Arabidopsis thaliana*. Mol Gen Genet 238:17–25

Zeng Q, Chen X, Wood AJ (2002) Two early light-inducible protein (ELIP) cDNAs from the resurrection plant *Tortula ruralis* are differentially expressed in response to desiccation, rehydration, salinity, and high light. J Exp Bot 53:1197–1205