

Chapter 1

Introduction

Dorothea Bartels, Ulrich Lüttge, and Erwin Beck

Evolution of life on earth began in aqueous environments. The oldest fossil records of green photosynthesizing organisms are the stromatolites of cyanobacteria-like organisms about 3.5×10^9 years old. One of the major problems organisms were facing when leaving the water and conquering the land 400×10^6 years ago in the Devonian was exposure to a dry atmosphere. Among the present land plants, we observe a wealth of structural and functional adaptations suitable for shaping the water relations appropriate for life under such conditions. However, even plants in the aqueous habitats may have been subject to dry periods given by tidal rhythms or temporary drying out of their aqueous habitat. As primary water plants and not having evolutionary adaptations, these organisms needed to acclimate to dehydration conditions, the most extreme one of which is survival of desiccation, i.e. the loss of most of the cellular water.

Organisms that tolerate desiccation by dormancy and resume metabolic activity upon re-wetting have been termed poikilohydric. Their water content varies since they respond to the humidity of their environment like physical systems by shrinking and swelling. Unlike the non-desiccation-tolerant so-called homoiohydrous organisms, they are not differentiated into organs for absorption of water and structures that prevent loss of water (Schulze et al. 2005).

To date, we find many desiccation-tolerant forms among extant prokaryotic cyanobacteria (Chap. 2) and eukaryotic green algae (division Chlorobionta), such as the Chlorococcales in the class Chlorophyceae and species of the classes Trebouxiophyceae and Trentepohliophyceae, as well as species of *Porphyridium* among the red algae (class Rhodophyceae) (Chap. 4). Hence, desiccation tolerance must have evolved early and polyphyletically. However, in these algal taxa it was a primary step in evolution. Therefore, we consider the desiccation-tolerant cyanobacteria and algae as well as basic cryptogamic land plants such as bryophytes, lichens and fungi (Chaps. 5–7) termed as “primary poikilohydric” species. Desiccation tolerance can be expressed in somatic cells but particularly in special survival units, i.e. cysts, spores and zygotes, often surrounded by thick cell walls. Evolution has maintained this in vascular plants where spores of pteridophytes, pollen grains and most seeds of gymnosperms and angiosperms are highly desiccation tolerant. In some cases, seeds can survive dryness for years, up to one or two centuries and in the famous case of lotus (*Nelumbo nucifera*) even 1,200 years

(Shen-Miller et al. 1995). While the germination success of the more than 10,000 years old Pyramid-wheat could not be substantiated, other seeds, e.g. from a date palm, which germinated and grew, have been dated more than 2,000 years BP (Sallon et al. 2008).

For the vegetative bodies of vascular plants, desiccation tolerance has evolved regressively or secondarily; these plants have been termed “secondary poikilohydric” (Chaps. 8 and 9). Secondary poikilohydric vascular plants are much fewer than the primary ones. They are predominantly found among the pteridophytes, the ferns and fern allies (700–1,000 species), but are rare in the angiosperms. Only a total of not more than 350 vascular poikilohydric angiosperm species have been described up to now (Chaps. 8 and 9). An impressive example of a secondary water plant, which is secondary poikilohydric, is the angiosperm *Chamaeigigas intrepidus* (Chap. 12). Evidently, secondary poikilohydry has also evolved polyphyletically, but these were rare events. Development of desiccation avoidance in the evolution of vascular land plants was the more effective strategy than of desiccation tolerance. The latter requires complex dehydration and rehydration machineries.

There is a trade-off between desiccation tolerance and the size of plants as most desiccation-tolerant plants do not grow into tall plants. Poikilohydric thallophyte tissues usually consist of smaller cells, and the water potential of their protoplasts and organelles is in equilibrium with that of their immediate environment. Terrestrial poikilohydric thallophytes may have stomata-like structures, e.g. some liverworts and hornworts; however, these are immovable vents and are not able to control water loss to the atmosphere. Shrinkage upon dehydration is less dramatic as with vascular plants, and as a consequence, the compartment of the thallophytes differs fundamentally from that of the desiccation-tolerant vascular plants when losing and regaining water during a desiccation/rehydration cycle (Chaps. 6 and 10). One of the tallest and best-studied desiccation-tolerant angiosperms is the small dicotyledonous shrub *Myrothamnus flabellifolia*. The tree habit is also reached by some desiccation-tolerant monocotyledons (Sect. 8.2.2).

For the desiccation tolerance of taller vascular plants, hydraulic architecture is an important aspect. Cavitation and the replacement of water by air (embolism; Chap. 10) in the conducting elements of the xylem are outstanding implications of drought and the more so upon desiccation in vascular plants. The consequences for resurrection during rehydration are intriguing and the mechanisms of refilling are unknown as of yet. Little work has been performed on resurrection plants. However, the transition from temporal tolerance of tight water relations to drought resistance and further to the tolerance of desiccation is gradual. From savanna trees, we know daily courses where water-stress-related midday depression of hydraulic conductivity is followed in the afternoon by cavitations and embolisms in roots and leaves, which are refilled during the night (Bucci et al. 2003; Domec et al. 2006). There are also annual courses: For example, in the fern *Mohria caffrorum* poikilohydry is developed seasonally, i.e. plants are desiccation tolerant in the dry season but not during the rainy season (Farrant et al. 2008). Thus, Chap. 10 evaluates the structures and functions relevant for water flow, from the cellular

to the organ and whole-plant level as an essential basis for any experimental approaches towards understanding their functional contribution to desiccation tolerance of vascular plants. One of the key points is indeed refilling of the conducting elements with water upon re-watering and during the process of resurrection. Often in nature extreme cases prove to be the best examples for understanding basic problems and Chap. 10 evidently ends up with the message that desiccation-tolerant plants are such an example challenging new research.

The poikilohydric cryptogams and among the vascular plants the majority of the poikilohydric ferns and dicotyledonous species retain their chlorophyll and much of the photosynthetic machinery during desiccation. They are termed “homoiochlorophyllous”. Among the monocotyledonous plants, we find both homoiochlorophyllous and poikilochlorophyllous species. The latter degrade their chlorophyll molecules as well as the thylakoid membranes during desiccation. In evolution, homoiochlorophyllous was primary and poikilochlorophyllous was secondary. Interestingly, in this respect, some plants are only partially homoiochlorophyllous like *Ramonda serbica* (Degl’Innocenti et al. 2008).

Light is the most critical stress factor during dehydration, in the desiccated state and upon rehydration (Chaps. 3 and 7). The problem of homoiochlorophyllous plants is that they are under severe stress of photodestruction by maintaining light absorbing pigment complexes, but their advantage is that they recover photosynthetic activity rapidly upon rehydration. The advantage of the poikilochlorophyllous plants is that by dismantling their photosynthetic apparatus they avoid photodestruction. Their problem is that upon rehydration there is a substantial lag phase before they are able to resume photosynthesis (Chap. 9). Although homoiochlorophyllous is considered to be a basic evolutionary trait, it does need a highly sophisticated machinery of photoprotection as it is described in several chapters (Chaps. 3, 7 and 11), while the more advanced trait of poikilochlorophyllous requires a complex set of molecular and biochemical mechanisms (Chaps. 9, 13–16). Good examples to this are the needles of the winter hardy evergreen conifers, which, upon crystallization of tissue water in the intercellular spaces, may lose more than 90% of their liquid cellular water. These plants degrade a major part of their antenna pigments in the course of frost hardening still before the onset of frost (Beck et al. 2004). For a homoiohydric plant, this extreme degree of dehydration is only tolerable at subfreezing temperatures when biochemical reactions are greatly slowing down or even cease.

Functional diversity is profoundly determined by the homoiochlorophyllous or poikilochlorophyllous nature of desiccation-tolerant plants. Poikilochlorophyllous determines the ecological niche acquisition by the respective species given by the extensions of dry periods (Chap. 9).

Thus, we face a large diversity in desiccation tolerance. This is covered in the various chapters of this book at different levels. At the phytogeographic level, we arrive at the diversity of habitats as an important facet (Chaps. 2, 4, 5 and 8). Ecological constraints of habitats determine selection of species. At the organismic level, we then consider the diversity of the organizational status of cyanobacteria, algae, bryophytes, lichens (Chaps. 2, 4 and 5) and vascular plants (Chap. 8). Functional

diversity is seen in a variety of mechanisms of evolutionary adaptation as well as more short-term ecophysiological acclimation.

We realize that understanding of desiccation tolerance at the organismic level and in an ecological context has been continuously advanced (Part II). At the cell biological level, we distinguish biophysical mechanisms and biochemical processes starting from gene expression to the activity of proteins and the accumulation or disappearance of metabolites, unravelled by the various components of the so-called “omics” that provide the information basis for systems biology. Advanced methodology for highly sophisticated analyses of the biophysical processes of excitation of the photosynthetic apparatus and the dissipation of the energy of the excitons produced fosters understanding of principal problems and their potential solutions of green desiccation-tolerant organisms (Chaps. 3 and 7). This has impact at the level of the organisms (Part II) but also forms a link to the cellular level (Part III). There, it is re-considered from a biochemical viewpoint addressing oxidative stress and its function in cell biology under water deficit (Chap. 11) and the apparently paradoxical special case of an aquatic poikilohydric angiosperm (Chap. 12).

The major section (Chaps. 13–16) of the cell biological Part III fathoms the relevance of the enormous progress of molecular biology and genetics for the understanding of desiccation tolerance. We must recall that in terms not only of adaptation during evolution but also of acclimation to recurrent or arrhythmic environmental changes responses to water shortage and pronounced drought with an eventual coronation by desiccation tolerance are gradual. Therefore, just like for hydraulic architecture (Chap. 10), we must realize at the level of cell biology that drought tolerance in many aspects appears as a prelude to desiccation tolerance. Therefore, although this volume focuses on desiccation tolerance, certain aspects of responses to drought must also be included. Many defence strategies, e.g. against damage from radicals, are similarly involved in both drought and desiccation tolerance, and responses to drought and desiccation are, therefore, often quite similar. Desiccation tolerance especially of vascular plants is considered as a more advanced adaptation to severe and temporal shortage of water than drought tolerance. *Sensu stricto* desiccation tolerance involves the survival of losing the major fraction of tissue water under exposure to dry conditions, and showing recovery of full physiological competence after rehydration. At the molecular level, mechanisms providing for drought and desiccation tolerance are shared with respect to the genetic management of input of stress signals and of downstream processes of damage, repair, tolerance and avoidance. This raises the strong demand of a new comprehensive treatment considering genomics, transcriptomics, proteomics and metabolomics moving on from drought-tolerant to desiccation-tolerant plant systems.

Thus, Chap. 13 sets the scene by delineating the basic concepts of functional genomics, epigenomics, genetics, molecular biology and the sensing and signalling networks of systems biology, which we need when we consider stress physiology in general and with particular focus on tight water relations. A specific component of the complement is highlighted in Chap. 14, namely the dehydrin proteins. They have multiple general functions as chaperones modulating and protecting

macromolecular cell structures and biomembranes. They occur in all seed plants and have been associated with the acquisition of desiccation tolerance of seeds. They are the best-characterized group of the so-called LEA proteins. LEA means “late embryogenesis abundant”, i.e. they abound in seeds that are normally desiccation tolerant. Is there an evolutionary link to desiccation tolerance of somatic tissues? At least for one *bona fide* resurrection plant, *Craterostigma plantagineum*, some evidence for the involvement of dehydrins is available (Sect. 14.10). Overexpression of a dehydrin from barley in rice has been shown to increase tolerance of specific water-deficit stresses (Xu et al. 1996). We certainly must have an eye on dehydrins when further fathoming the mechanisms of desiccation tolerance, and Chap. 16 picks up the LEAs again.

The desiccation-tolerant moss *Physcomitrella patens* is fully sequenced. However, we do not have complete genome sequences of desiccation-tolerant higher plants. When this advances, comparisons with the genomes of other model plants such as *Arabidopsis thaliana* (Chap. 13) will turn out to be highly profitable. It is remarkable, however, how Chap. 15 can already advance from the conceptual basis of Chap. 13 towards revealing constituents of systems biology of desiccation tolerance using genomics, proteomics, metabolomics and fluxomics. A wealth of relevant genes from resurrection plants is identified, and the involvement of their gene products can be described. This is already much pertinent information and generates knowledge. It gives the basis and shows the direction towards understanding.

As far as it is possible at this stage of the progress of research Chap. 16 then reassembles many of the putative constituents of the desiccation-tolerance complement linking molecular biology with physiology. The challenge for further endeavours of investigation is obvious. The reward these endeavours will give for understanding plants, habitats, natural ecosystems as well as agro- and forest-ecosystems and biomes where water is one of the most essential ingredients, is similarly obvious.

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