Ecological Studies 215

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Plant Desiccation Tolerance

Springer

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Volume 215
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Plant Desiccation Tolerance

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ISSN 0070-8356
ISBN 978-3-642-19105-3 e-ISBN 978-3-642-19106-0
DOI 10.1007/978-3-642-19106-0
Springer Heidelberg Dordrecht London New York

Library of Congress Control Number: 2011931204

Cover design: deblik Berlin, Germany

Printed on acid-free paper

Springer is part of Springer Science+Business Media (www.springer.com)

Foreword

'Dark brown shrivelled dead-looking leaves' 'so dry they can be crushed to a powder between one's fingers' 'the plant cost its own weight in gold' 'surprisingly, the rehydrating leaves became green again' 'the leaves expanded to ten times their area when they were dry' – these phrases display the astonishment evoked by the novel vision of a desiccation tolerant 'resurrection plant' passing from a moribund dry state to a healthy active life as it re-hydrates! Such amazement has now been matched by rapidly advancing scientific understanding.

Researchers from countries widely spread from Hungary to New Zealand set out current knowledge on desiccation tolerant plants. It is appropriate that this book includes contributions of many eminent plant scientists from Germany – for German botanists played a substantial role in the initial reports of angiosperm species with desiccation tolerant foliage and in the subsequent research into the mechanisms involved in the survival and recovery of air-dry leaves. The first reports, by the taxonomist Kurt Dinter, of four desiccation-tolerant angiosperm species consisted of mere asides in his descriptions of species in the flora of southwest Africa. Fuller comments on one of these species, *Chamaegigas intrepidus*, were published by H. Heil in 1924. Four decades later P. Hoffman, G.H. Vieweg and H. Ziegler demonstrated renewed photosynthesis in re-hydrated shoots of the African 'resurrection bush' *Myrothamnus flabellifolia*, one of the species Dinter recognised to be desiccation-tolerant.

Focused exploration for desiccation-tolerant plants has extended our knowledge of the floristic spread and the geographic range greatly. Even a cursory perusal of the chapter topics shows that the phenomenon is found in the full range of phyla of chlorophyll-containing species from prokaryotes and cryptogams to angiosperms. Relatively few species in any one phylum have received intensive study. Among the angiosperms, Dinter's species *Craterostigma plantagineum, Chamaegigas intrepidus*, *Myrothamnus flabellifolia* and *Xerophyta viscosa* have all received considerable but by no means exhaustive scientific attention, as has also *Sporobolus stapfianus* that was recognised as a desiccation-tolerant grass in 1970.

The present tome also displays how the scope of desiccation-tolerant plant studies has expanded to embrace ecological, evolutionary, physiological, biochemical and molecular biological areas. In the last two instances, the increasing knowledge of desiccation tolerance is being driven by the explosive growth in the technology and understanding in these fields. The first investigations of gene expression of drying and rehydrating resurrection plants were conducted in the Max Planck Institute at Köln by Professor Dorothea Bartels and her colleagues. I am indebted to Professor Bartels for guiding my first steps in this important aspect of desiccation tolerance. The rapid growth of this field has given us insights into the complex changes in mRNA complements and the proteome that support the survival of drying leaves and the revival of rehydrating plants, not only in the foliage but also in the pollen and seed of most spermatophytes. The investigations of a widening number of researchers active in this area have elucidated much about the compounds and processes implementing desiccation tolerance. Much remains to be discovered on the mechanisms of regulating the implementation of desiccation tolerance. The visual drama of desolate air-dry plants re-imbibing water, re-expanding and reviving is matched by the intellectual fascination of the enabling molecular machinery. I hold the hope that a full comprehension of the regulatory processes will lead to genetic transformation of crop and pasture species to enable them to express throughout the full vegetative plant the desiccation tolerance of their seed and pollen – and so bring a full knowledge of the phenomenon of desiccation tolerance to its fullest practical yield.

Melbourne, Australia Donald F. Gaff
January 2011

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Part I
Introduction

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 stromatolithes 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

U. Lüttge et al. (eds.), *Plant Desiccation Tolerance*, Ecological Studies 215,
DOI 10.1007/978-3-642-19106-0_1,

(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 *Chamaegigas 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, homoiochlorophylly was primary and poikilochlorophylly 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 homoiochlorophylly 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 poikilochlorophylly 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. Poikilochlorophylly 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.

References

Beck E, Heim R, Hansen J (2004) Plant resistance to cold stress: mechanisms and environmental signals triggering frost hardening and dehardening. J Biosci 29:449–459

Bucci SJ, Scholz FG, Goldstein G, Meinzer FC, da SL SL (2003) Dynamic changes in hydraulic conductivity in petioles of two savanna tree species: factors and mechanisms contributing to the refilling of embolized vessels. Plant Cell Environ 26:1633–1645

Degl'Innocenti E, Guidi L, Stevanovic B, Navari F (2008) CO_2 fixation and chlorophyll *a* fluorescence in leaves of *Ramonda serbica* during a dehydration–rehydration cycle. J Plant Physiol 165:723–733

Domec J-C, Scholz FG, Bucci SJ, Meinzer FC, Goldstein G, Villalobos-Vega R (2006) Diurnal and seasonal variation in root xylem embolism in neotropical savanna woody species: impact on stomatal control of plant water status. Plant Cell Environ 29:26–35

Farrant JM, Lehner A, Cooper K, Wiswedel S (2008) Desiccation tolerance in the vegetative tissues of the fern *Mohria cafforum* is seasonally regulated. Plant J 57:65–79

Sallon S, Solowey E, Cohen Y, Korchinsky R, Egli M, Woodhatch I, Simchoni O, Kislev M (2008) Germination, genetics, amd growth of an ancient date seed. Science 320:1464

Schulze E-D, Beck E, Müller-Hohenstein K (2005) Plant ecology. Springer, Berlin, pp 278–279

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

Xu D, Duan X, Wang B, Hong B, Ho T-HD WuR (1996) Expression of late embryogenesis abundant protein gene, HVA1, from barley confers tolerance to water deficit and salt stress, in transgenic Rice. Plant Physiol 110:249–257

Part II
The Organismic Level

Chapter 2
Cyanobacteria: Habitats and Species

Burkhard Büdel

2.1 Introduction

Cyanobacteria were most probably the first group of organisms performing an oxygen releasing photosynthesis. Their possible fossil origin ("look-alikes") from Apex chert of north-western West Australia dates back to about 3.46 billion years (Schopf 2000). However, the oldest unambiguous fossil cyanobacteria were found in tidal-flat sedimentary rocks and are about 2 billion years old (Hofmann 1976). With the onset of oxygenic photosynthesis between 2.45 and 2.32 billion years ago (Rasmussen et al. 2008), the ancient Earth's oxygen-free atmosphere experienced a deep impact with the sharp rise of oxygen. Before the evolution of respiration, the oxygen was highly toxic to life, and as a consequence, the first global catastrophe for most of the organisms living on earth to that date followed. Today, cyanobacteria are found in almost all habitats and biomes present on earth (Whitton and Potts 2000). However, to successfully colonize terrestrial habitats does also mean to be able to resist extreme desiccation. Air-drying does severely harm membrane structure, proteins, and nucleic acids and is lethal to the majority of organisms on Earth (Billi and Potts 2002). During their long evolutionary history, cyanobacteria developed the ability of their cells to undergo nearly absolute dehydration during air-drying without being killed, a phenomenon known as *anhydrobiosis*. This is also referred to as "desiccation tolerance" and is one mechanism of drought tolerance (Alpert 2005). Consequently, cyanobacteria colonized more and more of the available terrestrial habitats. Dehydration in air can lead to a removal of all but 0.1 g water/g dry weight (Billi and Potts 2000).

2.2 Cyanobacterial Anhydrobiosis and Resistance to Complete Desiccation

Desiccation-tolerant cyanobacteria must either protect cellular structures from damage and/or repair them upon rewetting. Dried aggregates of *Chroococcidiopsis* include live and dead cells, thus suggesting that desiccation resistance is not a

U. Lüttge et al. (eds.), *Plant Desiccation Tolerance*, Ecological Studies 215,
DOI 10.1007/978-3-642-19106-0_2, © Springer-Verlag Berlin Heidelberg 2011

simple process. In a recent study, Billi (2009) demonstrated that the desiccation surviving cells were avoiding and/or limiting genome fragmentation, preserve intact plasma membranes and phycobiliprotein autofluorescence, and exhibit spatially reduced reactive oxygen species accumulation and dehydrogenase activity upon rewetting. The percentage of cells avoiding subcellular damage was between 10 and 28% of dried aggregate. In the lichenized state, however, all cells of symbiotic *Chroococcidiopsis* species seem to survive desiccation, as there is no depression of photosynthetic CO_2 fixation rates of the same lichen thalli (genus *Peltula*, Lichinomycetes) before and after dry periods (Büdel et al. unpublished). This seems to be a general feature of lichenized cyanobacteria (Fig. 2.2g). The fungal host (mycobiont) apparently provides more than only a three-dimensional structure for optimized CO_2 and nutrient uptake, but also an environment for optimal (damage free) drying of cyanobacterial cells.

The common soil inhabiting cyanobacterium *Nostoc commune* Vaucher ex Bornet & Flahault developed protecting mechanisms to avoid genome fragmentation after prolonged cell desiccation (Shirkey et al. 2003). Changes at the ultra-structural level of *Chroococcidiopsis* cells have been demonstrated by Grilli Caiola et al. (1993). These authors could conclusively show that the thylakoid structure is changed in dry cells. The thylakoid double membrane opens between the single membranes, forming open spaces between them (Fig. 2.1a, b).

The filamentous, colony-forming cyanobacterium *N. commune* can tolerate simultaneous stresses of desiccation, UV irradiation, and oxidation. For protection, the acidic water stress protein A (wspA) and a highly stable and active

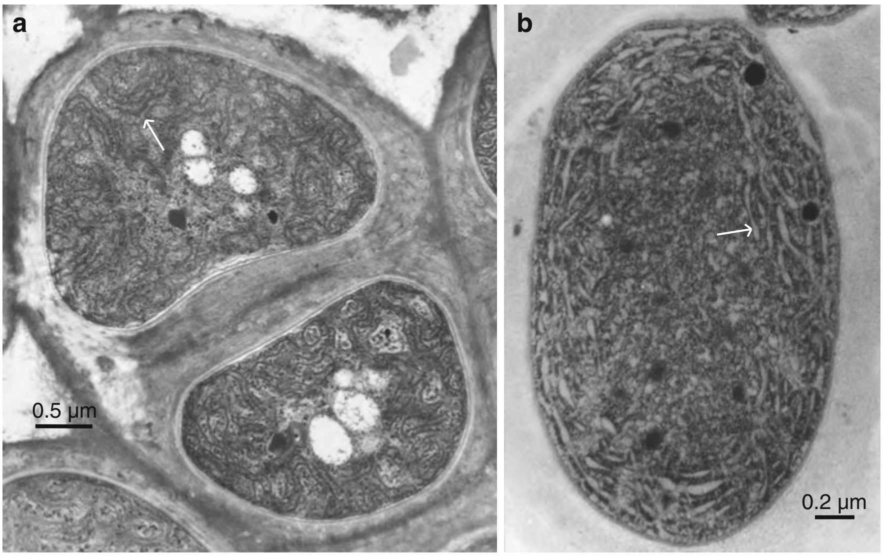

Fig. 2.1 Ultrastructure of wet and dry cells of the genus *Chroococcidiopsis*. (**a**) Wet cells, note the intact (closed double membrane layer) thylakoids (*arrow*). (**b**) Dry cell, freeze substituted over several months prior to ultrathin sectioning and microscopy in order to avoid preparation artifacts. Note the widened thylakoids (opening of the double membrane layer; *arrow*)

superoxidedismutase (sodF) were found to be secreted to the three-dimensional extracellular matrix. Transcription of wspA and sodF and synthesis and secretion of wspA were induced upon desiccation or UV-A/B irradiation of *N. commune* cells (Wright et al. 2005). The authors hypothesize that wspA plays a central role in the stress response of *N. commune* by modulation of structure and function of the three-dimensional extracellular matrix.

2.3 Habitats and Species

Once the importance of the microclimate for life conditions of small organisms was discovered, it soon became obvious that in terms of temperature, sunlight-exposed soils or rock surfaces are among the most extreme terrestrial habitats for photoautotrophic organisms (Kraus 1911; Jaag 1945). This led to the observation that two different exposures (SE versus NW in the northern hemisphere) on one large rock boulder can even result in a microclimate that reflects arctic alpine and sub-Mediterranean climates on one single rock (Schade 1917). As a result of high temperatures during insulation, lack of water and thus fast desiccation occurs in the colonizing organisms. Jaag (1945) showed that different rock types reach different surface temperatures under the same circumstances. At an air temperature of 16.5°C at 14:40 h in the Swiss capital of Zürich, he found surface temperatures of 35.7°C for diabas, 27.1°C for granite, and 24.4°C for marble during standardized measurements.

Cyanobacteria occur on almost all exposed rock surfaces on earth. There is hardly any rock surface to find without the presence of either epilithic (on the rock surface; Fig. 2.2d, e) or endolithic (inside the photic zone of the rock; Fig. 2.2a, c) growth of pro- or eukaryotic algae. Biofilms (thin smooth layers of pro- and eukaryotic algae only) or biological crusts (thick, uneven layers, often including lichens and sometimes bryophytes) occur on rocks of hot deserts (Büdel 1999; Büdel and Wessels 1991; Friedmann et al. 1967), polar deserts (Friedmann 1980; Broady 1981; Omelon et al. 2006; Büdel et al. 2008), inselbergs (Fig. 2.2c, d) in savannas and rain forests (Büdel et al. 2000), temperate regions (Boison et al. 2004), alpine zone (Horath and Bachofen 2009), and can even be found on the man-made surfaces of any kind of stone buildings (Eggert et al. 2006; Karsten et al. 2007).

A very conspicuous phenomenon of rock surfaces are the so-called Tintenstriche (German: Tinte = ink, Strich = stripe; Fig. 2.2e). They have been first described from the alpine habitat of the temperate region, but also occur in other biomes of the world (Lüttge 1997). Ink-stripes are bluish-black crusts on steep to more or less vertical rock surfaces such as dolomite (Diels 1914), granite (Golubic 1967; Büdel et al. 1994), sandstone (Wessels and Büdel 1995), and other rock types (Jaag 1945). The ink-stripe communities are dominated by cyanobacteria, sometimes accompanied by eukaryotic algae, fungal hyphae, and lichens, even mosses, and vascular plants can occur (Jaag 1945; Wessels and Büdel 1995). When studied under the light microscope, many cyanobacterial species expose very colorful sheaths (Fig. 2.3c, d, f, g). The bright yellow and red color mainly originates from scytonemin, an indol-alkaloid serving as light and UV protection (Buckley and Hougthon 1976; Garcia-Pichel and Castenholz 1991). When exposed to frequent desiccation