Plant Science 182 (2012) 29–41

Contents lists available at ScienceDirect

Plant Science

journal homepage: www.elsevier.com/locate/plantsci

Review

Photosynthesis in desiccation tolerant plants: Energy metabolism and antioxidative stress defense

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ARTICLE INFO

Article history:
Received 2 November 2010
Received in revised form 10 January 2011
Accepted 27 January 2011
Available online 5 February 2011

Keywords:
Resurrection plants
Desiccation tolerance
Photosynthesis
Reactive oxygen species
Oxidative stress

ABSTRACT

Resurrection plants are regarded as excellent models to study the mechanisms associated with desiccation tolerance. During the past years tremendous progress has been made in understanding the phenomenon of desiccation tolerance in resurrection plants, but many questions are open concerning the mechanisms enabling these plants to survive desiccation. The photosynthetic apparatus is very sensitive to reactive oxygen species mediated injury during desiccation and must be maintained or quickly repaired upon rehydration. The photosynthetic apparatus is a primary source of generating reactive oxygen species. The unique ability of plants to withstand the oxidative stress imposed by reactive oxygen species during desiccation depends on the production of antioxidants. The present review considers the overall strategies and the mechanisms involved in the desiccation tolerance in the first part and will focus on the effects on photosynthesis, energy metabolism and antioxidative stress defenses in the second part.

Contents

Abbreviations: ABA, abscisic acid; APX, ascorbate peroxidase; CAT, catalase; GR, glutathione reductase; LEA, late embryogenesis abundant proteins; MDAR, monodehydroascorbate reductase; ROS, reactive oxygen species; SOD, superoxide dismutase.

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doi:10.1016/j.plantsci.2011.01.018

1. Introduction

Dehydration is a very common stress among various abiotic stresses encountered by plants. Since water is the major limiting factor for growth and reproduction in plants, it is not possible for the plants to maintain cellular homeostasis and withstand dehydration without losing the turgor in the cells during periods of prolonged water deficit. Water deficit causes metabolic disruption and mechanical damage of membranes due to the generation of free radicals [1,2]. Desiccation tolerance is most frequently observed in mature seeds or pollen of higher plants but very rarely observed in other plant tissues. Pollen grains lose tolerance quickly, whereas seeds can stay longer in the desiccated state [3]. Remarkable is a group of vascular angiosperm plants termed "resurrection plants" which have an extraordinary ability to survive almost complete dehydration of their vegetative tissues and which regain a biologically functional state after rehydration. These plants are regarded as desiccation tolerant plants.

Desiccation tolerance is observed throughout the microbial, fungal, animal and plant kingdoms [4,5]. In the plant kingdom this process is widespread and is found in most of the taxonomic groups ranging from pteridophytes to dicotyledons but not observed in gymnosperms [6–8]. The mechanisms of desiccation tolerance in lower order resurrection plants like lichens, algae and bryophytes differ from those present in angiosperms [9,10]. Since desiccation tolerance in plants relies on the protection of cellular integrity and the repair of dehydration or rehydration induced damage [11], the resurrection plants are classified into two types based on the time required for the repair and recovery. Lower order plants such as *Tortula ruralis* (moss) which desiccate rapidly in about 1 h rely on constitutive damage and repair mechanisms during rehydration and are therefore classified as full desiccation tolerant plants as tolerance is unaffected by the rate of drying [9]. In contrast, higher order plants rely on the induction of mechanisms to protect cellular integrity during water loss and are classified as modified desiccation tolerant plants, since a certain amount of time is required for the induction of tolerance [9,12]. Several species, including *Craterostigma plantagineum*, *Craterostigma wilmsii*, *Myrothamnus flabellifolia*, *Eragrostis nindensis*, *Sporobolus stapfianus*, *Xerophyta viscosa* and *Xerophyta humilis*, have been intensively studied with the goal to identify the mechanisms responsible for their remarkable desiccation tolerance. Table 1 shows the list of different resurrection plants that have been analysed to decipher the mechanisms leading to desiccation tolerance.

Desiccation tolerant species are found in ecological niches with limited seasonal water availability, unreliable rainfalls and in soils with minimal water retention preferentially on rocky outcrops at low to moderate elevations in tropical and subtropical zones. These are found in all continents and in all growth forms except trees, but it remains a mystery why desiccation tolerance is not more widespread among higher plants [13]. A rich diversity of resurrection plants is found in Southern Africa (especially South Africa, Namibia and Zimbabwe), a region of significant arid and semi-arid areas [6].

Oxidative stress is one of the most deleterious consequences of water deprivation. Oxidative stress generated due to enhanced production of reactive oxygen species (ROS) especially by chloroplasts is minimized in resurrection plants by controlled shutdown of photosynthesis early during drying and by degradation of photosynthetic structures in some species. These plants are also endowed with low-molecular antioxidant molecules (i.e., ascorbate and glutathione) and antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) and glutathione reductase (GR) which catalyze the elimination of activated oxygen molecules to defend themselves against ROS [14,15]. Overall desiccation tolerant plants must be able to limit the damage caused by desiccation to a repairable level, maintain the physiological integrity and mobilize mechanisms upon rehydration that repair damage caused during desiccation and subsequent rehydration [16,17]. The mechanisms that confer desiccation tolerance include the production of non-reducing sugars, the synthesis of dehydrin proteins as well as the use of free radical scavenging systems [18]. Fig. 1 shows the different reactions taking place in resurrection plants during desiccation. Recently, some comprehensive reviews have been published emphasizing the molecular aspects of desiccation tolerance in resurrection plants [3,18–21]. This review presents an overview of the processes occurring in resurrection plants during desiccation emphasizing the effect of desiccation on photosynthesis, energy metabolism and antioxidative stress defenses.

2. Strategies of resurrection plants to cope with desiccation

Desiccation tolerance is a very complex multigenic and multifactorial process involving a combination of genetic, metabolic and antioxidant systems as well as macromolecular and structural stabilizing processes [19]. It is not an easy task for an organism to be alive after losing more than 90% of its cellular water upon dehydration and continue to grow after rehydration. The probability of cellular damage increases during desiccation, so these plants rely on the induction of mechanisms to protect and maintain the cellular integrity.

Table 1
List of the best studied resurrection plants to decipher the mechanisms for desiccation tolerance.

Name	Family	Class	Origin	Homoiochlorophyllous (H) or poikilochlorophyllous (P)	Reference
Craterostigma plantagineum	Scrophulariaceae	Dicot	Southern Africa	H	Rodriguez et al. [115]
Craterostigma wilmsii	Scrophulariaceae	Dicot	South Africa	H	Cooper and Farrant [11]
Lindernia brevidens	Linderniaceae	Dicot	East Africa	H	Phillips et al. [220]
Myrothamnus flabellifolia	Myrothamnaceae	Dicot	Southern Africa	H	Kranner et al. [188]
Boea hygrometrica	Gesneriaceae	Dicot	China	H	Jiang et al. [190]
Ramonda serbica	Gesneriaceae	Dicot	Serbia	H	Veljovic-Jovanovic et al. [208]
Haberlea rhodopensis	Gesneriaceae	Dicot	Balkan mountains (Bulgarian and Serbian)	H	Georgieva et al. [151]
Xerophyta viscosa	Velloziaceae	Monocot	Southern Africa	P	Ingle et al. [209]
Xerophyta humilis	Velloziaceae	Monocot	Southern Africa	P	Collett et al. [128]
Sporobolus stapfianus	Poaceae	Monocot	Southern Africa	–	Martinelli [88]
Eragrostis nindensis	Poaceae	Monocot	Southern Africa	P	Vander Willigen et al. [25]
Selaginella bryopteris	Selaginellaceae	Lycophyte	India	H	Pandey et al. [210]
Selaginella tamariscina	Selaginellaceae	Lycophyte	China	H	Liu et al. [69]
Selaginella lepidophylla	Selaginellaceae	Lycophyte	North and South America	H	Brighigna et al. [26]
Tortula ruralis	Pottiaceae	Bryophyte (Moss)	North America	H	Oliver et al. [48,221]

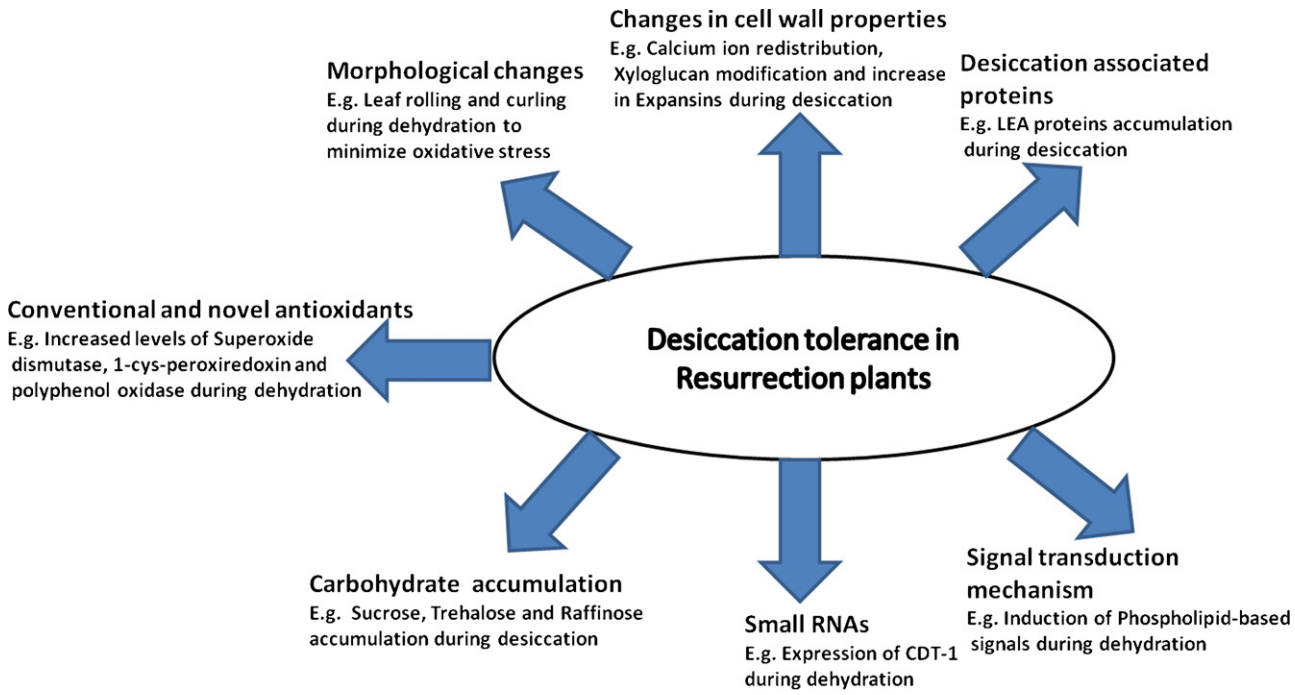

Fig. 1. Changes observed during desiccation in resurrection plants.

2.1. Morphological changes

During dehydration in resurrection plants, morphological changes in vegetative tissues occur to minimize the damage caused by excessive generation of free radicals [18]. Among these, leaf curling or folding is the preliminary and the most obvious change observed [22–25]. Leaves of *C. plantagineum* or *C. wilmsii* 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 and become fully expanded upon rehydration [14]. These movements of the leaf along with the leaf folding are thought to reduce the transpiring surface and limit oxidative stress damage from UV radiation and is thus an important morphological adaptation [26,27].

2.2. Modifications in cell wall properties

During desiccation cells shrink and a considerable reduction in tissue and cell volume takes place thereby causing severe mechanical stress [28]. A reverse phenomenon can occur upon rehydration when the water rushes into the cells and cells expand again. Desiccation tolerance requires the plant membranes to withstand the mechanical stress caused by the shrinkage of cells during dehydration and cellular expansion caused by reabsorption of water during rehydration. The major factor that contributes towards mechanical stabilization during desiccation appears to be the folding of cell walls. It has been reported that the cell volume of *C. wilmsii* decreased significantly upon desiccation [28] accompanied by a concomitant withdrawal of the plasma membrane from the cell wall as well as extensive cell wall folding. The shrinkage of the cytoplasm during desiccation creates tension between the plasmalemma and the cell wall which can result in tearing of the plasmalemma causing irreversible damage. To overcome this, several modifications occur to stabilize cell wall architecture in resurrection plants. Some of the modifications are inducible whereas some are constitutive. In *Craterostigma* and *Selaginella*, cell walls from the leaf tissues fold in along with the cell contents and become highly convoluted when desiccated and upon rehydration the cells return to their original volume without any visible injuries [29–31]. This folding of the cell wall is a strategy to avoid the tearing of the plasmalemma from the cell wall so that the integrity is maintained. Studies of the cell wall architecture indicated that the leaves of *C. wilmsii* possess a large proportion of homogalacturonan along with rhamnogalacturonan with calcium ion redistribution and xyloglucan modification which enhances strength and flexibility [18,32,33]. The increase in calcium during dehydration in cell walls is suggested to cross-link cell wall polymers such as acidic pectins and further stabilize the cell wall in the dry state [18,34]. In the case of *C. plantagineum*, expansins which are cell wall loosening factors are believed to be involved in cell wall restructuring [35,36]. Recent findings indicate that dehydration induces significant alterations in the polysaccharide content and structure of the cell wall of *C. wilmsii* which in turn may be involved in the modulation of the mechanical properties of the cell wall during dehydration [18]. In *M. flabellifolia* the pectin-associated arabinans and/or arabinogalactan proteins are important in keeping the cell wall flexible during desiccation.

2.3. LEA proteins

It is widely believed that protection during desiccation is afforded by the accumulation of various proteins, sugars and compatible solutes which serve to replace water and stabilize the sub-cellular environment by vitrification [37]. Late embryogenesis abundant (LEA) proteins represent an important group of hydrophilic proteins which accumulate to high levels during the late states of embryogenesis in seeds when desiccation tolerance is acquired or in vegetative and reproductive tissues under dehydration suggesting a role in adaptation during desiccation [38]. These proteins are predicted to have several protective functions which include protection of DNA, stabilization of cytoskeletal filaments and acting as molecular chaperones to protect protein conformation and activity [39]. These are unable to protect the proteins from heat shock and they also cannot recover the activity of the proteins that are lost during dehydration process suggesting their role in the maintenance of protein activity and function during dehydration [40]. It has also been shown that these proteins

can act synergistically with sugars, such as trehalose to prevent protein aggregation during desiccation [41]. Most LEA proteins are part of a more widespread group of proteins called "hydrophilins" which are characterized by a glycine content greater than 6% and a hydrophilicity index greater than 1. Members of the LEA protein families appear to be ubiquitous in the plant kingdom. Their presence has been confirmed not only in angiosperms and gymnosperms but also in seedless vascular plants and even in bryophytes, pteridophytes and algae [42–53]. In addition, similar proteins are found in bacteria and yeast [54,55], nematodes [56,57] and fungi [58,59]. The expression of LEA proteins along with dehydration-induced genes is regulated by abscisic acid [60–62]. In *C. plantagineum* at least two LEA proteins CDeT 11-24 and CDeT 6-19 are phosphorylated *in vivo* during desiccation [63]. Besides LEA proteins, other molecules such as small heat shock proteins and polyphenols (gallolylquinic acids) have similar properties [64–66]. They have been shown to protect membranes against desiccation suggesting the possible existence of other novel components with LEA protein like functions in resurrection plants. Recent reviews of Tunnacliffe and Wise [67] and Battaglia et al. [68] describe in detail the features and the functions of the LEA proteins with regard to desiccation tolerance.

2.4. Carbohydrates and desiccation tolerance

In most cases, the ability of the plant to survive desiccation correlates with the accumulation of carbohydrates. If carbohydrates have a protective role then they must be able to accumulate very rapidly and in sufficient quantity. So the time required for the carbohydrate accumulation becomes a crucial parameter during dehydration. Accumulation of sucrose, trehalose as well as raffinose is commonly observed in dehydrating resurrection plants [61] out of which trehalose occurs predominantly in desiccation-tolerant lower organisms including some vascular plants such as *Selaginella tamariscina* [69] and the moss, *T. ruralis* [70]. Sucrose and raffinose are found in all angiosperms [23,71–76]. In some of the resurrection plants sucrose accumulates as a product of photosynthesis [77] whereas *Craterostigma* species have evolved a specific mechanism of sucrose accumulation. *C. plantagineum* and *C. wilmsii* have a high level of eight carbon sugar, 2-octulose in leaves under well-watered conditions [78,79], upon dehydration the massive conversion of 2-octulose to sucrose takes place. This conversion is directly correlated with an increase in the expression of sucrose synthase and sucrose phosphate synthase [80,81] which result in the redirection of carbon flow from reserve substances such as starch or octulose to soluble saccharides such as sucrose. Thus *Craterostigma* has the capacity to accumulate sucrose very rapidly from carbohydrate sources already present in the leaf rather than relying upon photosynthesis. The presence of 2-octulose appears to act as a storage carbohydrate like starch in most C_3 plants since *Craterostigma* plants do not accumulate starch [82]. In these plants transketolases are thought to participate in the synthesis of octulose [83]. cDNA encoding these enzymes were isolated and expression analysis showed that *tkt*3 is constitutively expressed in leaves and roots whereas *tkt*7 and *tkt*10 are highly expressed in rehydrating leaves [84]. Also during dehydration and rehydration, mRNA concentrations of glyceraldehyde phosphate dehydrogenase and transketolase have been shown to increase in *Craterostigma* plants [84,85]. These suggest the preparedness of these plants to survive dehydration. Illing et al. [86] suggested that the breakdown and mobilization of oligo- and polysaccharides during dehydration provide the carbon skeletons necessary for sucrose synthesis. Upon dehydration in *X. viscosa* the accumulation of sucrose correlated with the increase in the activity of hexokinase and the removal of glucose and fructose [74,87]. A recent report by Martinelli [88] suggests that the glucose and sucrose accumulate in specific locations in resurrecting plant tissues during dehydration and function to protect chloroplast and tonoplast membranes from desiccation. The role of sucrose in protecting membranes and stabilizing biomolecules was suggested by Crowe et al. [37] and Martinelli [88].

2.5. Small regulatory RNAs

The significance of small RNAs in regulating plant responses to abiotic stress is now widely accepted [89,90]. Bartels et al. [60] demonstrated that the application of exogenous ABA was able to induce desiccation tolerance in callus of *C. plantagineum*. Constitutive expression of CDT-1, a dehydration and ABA-inducible gene led to desiccation tolerance in callus and to the constitutive expression of dehydration and ABA responsive transcripts in *C. plantagineum* in the absence of ABA treatment [90]. CDT-1 and other functionally related gene members have features of a short interspersed element retrotransposon and are hypothesized to act as regulatory non-coding RNA molecules which are unique to *C. plantagineum* [91].

2.6. Signaling mechanisms

The general stress signal transduction in plants starts with the perception of the stress signal followed by the generation of secondary messengers which modulate the intracellular Ca^{2+} often initiating a protein phosphorylation cascade and finally targeting proteins involved in cellular protection or transcription factors controlling transcription of stress regulated genes. The products of these genes may participate in the generation of regulatory molecules like the phytohormone, abscisic acid (ABA). Accumulation of ABA is one of the earliest responses observed in plants under drought stress. Apart from being a key player in the induction of desiccation tolerance, ABA regulates the expression of proteins such as LEA proteins [61,92]. ABA has also been shown to be associated with the expression of several dehydration-regulated genes in resurrection plants [60–62,93–96]. The information about genes that are involved in signaling and regulatory pathways in resurrection plants is limited in comparison to *Arabidopsis*. In *C. plantagineum*, the synthesis of phospholipid-based signaling molecules is one of the earliest events in the perception of water stress [97]. Two cDNA clones encoding phospholipase D have been isolated from *C. plantagineum* whose activity is induced by dehydration but not by ABA. The constitutively expressed *CpPLD-1* transcript is thought to be involved in early responses to dehydration by producing second messenger molecules, whereas the dehydration-induced *CpPLD-2* might be involved in phospholipid metabolism [97]. In addition several classes of dehydration induced transcription factors have been isolated from *C. plantagineum* such as myeloblastosis (MYB) family [98], homeodomain-leucine zipper (HD-Zip) family [99,100], basic leucine zipper family [101] and a novel zinc finger factor [102].

3. Response of photosynthesis to dehydration

Photosynthesis, a complex metabolic process is very well known to be affected by dehydration. In response to water stress, a decrease in net CO_2 assimilation is generally observed which can be the result of decreased CO_2 availability for Rubisco caused by restricted diffusion through stomata and mesophyll [103,104]. The decrease in Rubisco activity, generally observed during water stress, is mainly due to decreased stomatal conductance and chloroplastic CO_2 concentration rather than decreased relative water content [105]. Transcripts encoding the small subunit of Rubisco were reported to be downregulated in response to water stress [106]. The decline in photosynthesis can also be due to the alterations in photosynthetic metabolism [107], by

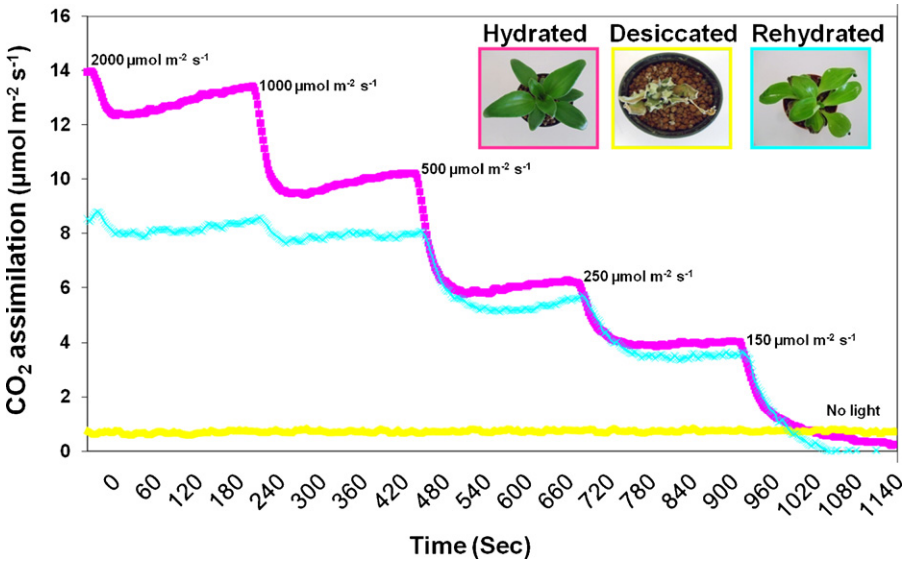

Fig. 2. The photosynthetic CO_2 assimilation rates monitored in hydrated, completely desiccated and rehydrated plants (48 h) of *C. plantagineum* using the GFS 3000 portable photosynthetic system. The light intensities were set from 150 to 2000 µmol m^{-2} s^{-1} in the instrument and the photosynthetic rates were monitored at different time points. The pink curve depicts the photosynthetic rate in a hydrated plant, the yellow curve is from a desiccated plant and the blue curve is from a rehydrated plant. For rehydration, desiccated plants were submerged in water for 48 h before measuring the photosynthetic rate. (For interpretation of the references to color in the figure caption, the reader is referred to the web version of the article.)

limitation in the generation of reducing power or in the metabolic activity thereby seriously affecting photosynthetic machinery. The photosynthetic apparatus is very sensitive to injury during dehydration and maintenance of it in a recoverable condition throughout the dehydration process or quick repair upon rehydration is necessary for restoring photosynthetic activity. Thus, the physical properties of the photosynthetic apparatus are of crucial importance in desiccation tolerant plants. The light energy absorbed by chlorophyll cannot be dissipated via photosynthesis under water limited conditions and thus can lead to the formation of reactive oxygen species (ROS) [108–110]. The angiosperm resurrection plants avoid the toxic build-up of ROS by controlling the metabolism and shutting down photosynthesis during desiccation [14,28]. Upon rehydration the photosynthetic capacity is fully recovered. In agreement with this, leaves of *Ramonda serbica* and *Haberlea rhodopensis* showed a remarkable decrease in photosynthetic CO_2 assimilation upon desiccation and on rehydration the photosynthetic rate was completely recovered. It was suggested that the decrease in photosynthesis during desiccation in these leaves is not only due to stomatal closure but also due to reduced CO_2 photoassimilation [111–113]. The recovery of CO_2 assimilation during rehydration was positively correlated with an increased stomatal conductance and Rubisco activity. A similar response is observed in *C. plantagineum*, where desiccation decreased the photosynthetic rates significantly while rehydration restored the photosynthetic activity (Fig. 2). The catalytic activity of Rubisco is restored and regulated by Rubisco activase: a molecular chaperone whose activity is dependent on higher stromal ATP/ADP ratio [114]. The decrease in the activity of Rubisco is more related to the activity of Rubisco activase and ATP/ADP ratio than to the changes at protein level. In *C. plantagineum*, the transcripts encoding Rubisco activase were reported to be abundantly expressed in untreated plants suggesting that the plant is prepared to respond to dehydration [115]. Recent studies indicated that Rubisco activase plays a vital role in response to photosynthesis to temperature stress [116–118] but studies on the regulation of Rubisco activase during dehydration and rehydration are very limited for resurrection plants.

It is already apparent that a significant number of genes related to photosynthetic metabolism are affected by desiccation [115]. The mechanisms of shutting down the photosynthesis in resurrection plants appear to vary among species. In this context we cannot neglect the importance of maintaining the intactness of membranes or repairing them for carrying on the electron transport reactions. As an example, the thylakoids from spinach were ruptured when leaves were exposed to wilting or freeze–thaw cycle [119] and upon rewatering, the thylakoid membranes were no longer functional and turgidity was completely lost. Contrary to this, in desiccation tolerant plants complete recovery of turgidity and the restoration of membrane functions were observed upon rehydration [120,121]. Many studies have indicated that the photochemical reactions are sensitive indicators to study the physiological state of resurrection plants during desiccation and rehydration [14,112,122]. The energy transfer to the reaction centers of PS II and PS I results in electron transfer to ferredoxin and then reduction of $NADP^+$. The limitation of photosynthetic carbon fixation during dehydration decreases the utilization of NADPH with a decline in the $NADP^+$ level, a major acceptor of electrons in PS I. Depletion of $NADP^+$ accelerates the transport of electrons from PS I to molecular oxygen and the generation of ROS [114]. The damage to the oxygen-evolving complex of photosystem II (PS II) and to the PS II reaction centers is commonly observed in water-stressed plants [123–125]. Among the thylakoid reactions, electron transfer from PS II is responsible for the water splitting and oxygen evolving functions in photosynthesis. The loss of PS II function correlates with the loss of power to generate potentially damaging reactants and therefore it acts as a sensor for stress [125,126]. The integrity of thylakoids and the amount and ratio of pigment–protein complexes are maintained, although the photosynthetic carbon fixation and the PS II functions are decreased in dehydrated *Boea hygrometrica* and *H. rhodopensis* [112,127]. The significant decrease in PS II activity in *R. serbica* leaves upon desiccation was suggested to be a protective mechanism to maintain membrane integrity [113]. In *X. humilis*, low levels of *PsbA* transcript, which constitute the reaction center protein D1 and is required for initial assembly of PS II is stably maintained during desiccation. In these plants

the recovery of PS II is independent of transcription, since the necessary transcripts are stored for immediate translation within the first phase of rehydration [128]. Among the different classes of desiccation-induced proteins which seem to be involved in the maintenance of chloroplast stability [129–131] LHC proteins (primary chlorophyll-binding proteins) are considered to be important.

The decrease in net CO_2 assimilation during cellular dehydration correlates with the decrease in cellular ATP levels which in turn is related to the decrease in ATP synthase [132]. Although the photosynthesis is downregulated, cellular ATP is not fully depleted because respiration continues in water-stressed leaves. Generally 30% of the ATP content is maintained in stressed leaves when compared with non-stressed leaves. The chloroplastic ATP synthase, responsible for coupling ATP synthesis and hydrolysis to the light driven electrochemical proton gradient, comprises CF_0 and CF_1 components, out of which CF_0 is embedded in the thylakoid membrane and CF_1 is projected into the chloroplast stroma. The movement of protons due to the difference in pH between thylakoid lumen and stroma causes the physical rotation of these components thereby altering the conformation of the active enzyme site and synthesizing ATP. The ionic concentrations affect ATP synthase and binding between CF_0 and CF_1 *in vivo* [132]. Due to the increase in the ionic concentration, the dissociation of the CF_1 component of ATP synthase the thylakoids lose the capability for light dependent ATP synthesis during water stress [133]. As an example, increased magnesium concentrations decrease photophosphorylation of chloroplasts isolated from stressed leaves [132]. The observations of Schwab et al. [133] and Georgieva et al. [112] suggest that the Calvin-cycle enzymes are more affected by dehydration than membrane bound electron transport reactions. In the recent years reviews have been published which gave a detailed description on the effects of water stress on photosynthesis and related metabolic processes [107,114,134–136] but to our knowledge the coverage of photosynthesis in resurrection plants is very limited.

4. Homoiochlorophyllous and poikilochlorophyllous resurrection plants

The differences in the behavioural patterns of photosynthetic apparatus led to the categorisation of desiccation tolerant plants into two groups, i.e., homoiochlorophyllous plants and poikilochlorophyllous plants (Table 1 [22,137,138]). Poikilochlorophylly is mostly observed within monocots and currently known in eight genera of five families (Boryaceae, Cyperaceae, Poaceae, Schizaeaceae, and Velloziaceae) whereas, homoiochlorophyllous plants include species from five families of pteridophytes (Actiniopteridaceae, Aspleniaceae, Pteridaceae, Selaginellaceae, and Sinopteridaceae), and four families of dicotyledons (Gesneriaceae, Myrothamnaceae, Scrophulariaceae and Linderniaceae). One species of Cactaceae, namely *Blossfeldia liliputana*, is desiccation-tolerant and represents the unique form of a succulent resurrection plant [13,139]. Homoiochlorophyllous species, e.g. *Craterostigma* spp. retain the chlorophyll and thylakoid membranes intact during desiccation, although changes in photosynthetic pigment distribution were observed [140]. The chloroplasts in these plants become round, with altered inner membrane organisation along with the change in the ratio between lipids and proteins and between different lipids that occur in thylakoid membranes [28,31,129,141]. In vascular homoiochlorophyllous plants, photochemical activity has been reported to be maintained longer during drying than CO_2 assimilation [133]. Though the carbon fixation is inhibited during drying the photo-excitation of chlorophyll responsible for the production of ROS persists [142]. In *C. wilmsii* and *M. flabellifolius* the photosynthesis is switched off during drying, due to chlorophyll shading through leaf folding and anthocyanin accumulation [28]. In these plants the rehydration can occur in a single leaf or a leaf disc detached from the plant.

In poikilochlorophyllous species, e.g. *Xerophyta*, the thylakoid membranes are dismantled, chlorophyll and the photosystem complexes are broken down upon desiccation [28,137]. The degradation of chlorophyll is advantageous in these plants since the accumulation of toxic ROS is reduced. During dehydration chloroplasts lose chlorophylls, most carotenoids and the entire thylakoid system. As a consequence the whole photosynthetic apparatus must be reconstructed following rehydration [143,144]. Pigment loss and destruction of the other thylakoid pigments are highly organised responses to desiccation, realised via a well-defined metabolic pathway [137]. This offers an advantage to homoiochlorophyllous plants that they resume photosynthesis faster than poikilochlorophyllous species which have to synthesize all components *de novo*. The poikilochlorophyllous leaves cannot resurrect when they are detached from the plant in contrast to homoiochlorophyllous resurrection plants.

5. Responses of photosynthesis to dehydration under low and high light

Under water-deficit stress in high-light conditions, the excitation energy by chlorophyll can greatly exceed the demand of the Calvin cycle for ATP and NADPH, leading to overreduction of the electron transport chain and enhanced generation of ROS [109,145,146] thereby leading to inhibition of PS II reaction centers [147], damage to the ATP synthesizing machinery [136] and ultimately decreasing the photosynthetic rate [107]. Angiosperm resurrection plants prevent the absorption of excess light and accumulation of free radicals by leaf movements and also by various cellular defense reactions (Fig. 1 [14]). Enhanced susceptibility to photoinhibition is observed in the desiccation tolerant resurrection fern *Polypodium polypodioides* and *H. rhodopensis* upon desiccation and the recovery after rehydration is delayed [148,149]. Desiccation of *H. rhodopensis* at very low light ($30\ \mu mol\ m^{-2}\ s^{-1}$) irradiance led to a minor decrease in the levels of D1, D2 and PsbS and PsaA/B proteins in thylakoids, but a relative increase in LHC polypeptides [112,150], upon rehydration the plant recovered perfectly. The photosynthetic proteins remained comparatively stable in the desiccated stage under low light whereas they were destroyed in desiccation sensitive plants. Dehydration of *H. rhodopensis* plants under moderate light ($100\ \mu mol\ m^{-2}\ s^{-1}$) decreased the quantum efficiency of PS II photochemistry and the rate of net CO_2 assimilation more than the dehydration at low light intensity and is rehydrated completely [151]. The recovery was more rapid in low light grown plants than in moderate light grown plants. The loss of photosynthetic activity during dehydration was faster in moderate light plants than at low light plants. Contrary to the situation observed in low light and moderate light plants, irreversible damage in the structure and function of the photosynthetic apparatus was observed during desiccation at high light ($350\ \mu mol\ m^{-2}\ s^{-1}$) intensity [151,152], the leaves did not recover after rehydration. The photosynthetic activity was completely restored in low light desiccated plants after one week of rehydration, but changes persisted under high light conditions. The greater resistance of the photosynthetic apparatus to low light than to moderate light and high light suggests that desiccation is strongly affected by light conditions and also shows the negative effect of light intensity on the rehydration process. The appearance of dense luminal substances in the thylakoid lumen during desiccation and recovery under low light were suggested to protect the leaves from oxidative damage. The disappearance of the dense luminal substance during desiccation under high light correlated with the oxidative damage and ceased the recovery of photosynthesis upon rewatering [151].

Desiccated *T. ruralis* gametophytes under darkness, low light ($50\,\mu mol\,m^{-2}\,s^{-1}$) or high light ($1500\,\mu mol\,m^{-2}\,s^{-1}$) intensities were also utilised to investigate the interaction between the light intensity and desiccation/rehydration cycle upon ELIP expression [153]. ELIPs were discovered to be transiently expressed during the greening of etiolated plants [154] and are nuclear encoded light inducible proteins detectable within the thylakoid membrane systems [155]. ELIP proteins accumulate in green tissues in response to a variety of environmental cues such as high light [156,157], desiccation [93] and other stress conditions. They are similar to the HLIPs (high light induced proteins) of cyanobacteria and the LHC (light harvesting complex) proteins of photosystems. ELIPs bind to chlorophylls in order to keep free pigments at low levels in conditions of high light stress [158]. Earlier reports also suggested that ELIPs might bind zeaxanthin, taking part in the non-photochemical quenching of light energy [159]. Upon drying in high light the higher accumulation of *Elipa* transcripts relative to darkness and low light was observed in *T. ruralis* gametophytes. Rehydration caused the increase in steady state transcript levels of *Elipa* and *Elipb* only when gametophytes were rehydrated under high light confirming the key role played by ELIPs in the protection and repair of the photosynthetic apparatus under HL conditions [153]. Several of the stress-induced proteins in *C. plantagineum* are transported to the chloroplasts and are supposed to exert their protective function within these organelles [93,129]. Examples of chloroplast protective proteins are pcC 37-31 (a chloroplastic protein homologous to ELIP proteins [93]), pcC 3-06 (localized in the stroma of chloroplasts, partially homologous to group 3 *LEA* genes [160]) and pcC 13-62 (associated with thylakoid membranes, homologous to an *Arabidopsis* cDNA clone [129,161]). Furthermore, a novel gene family of chloroplast targeted proteins which is expressed very rapidly and transiently in chloroplasts in response to dehydration and to ABA was identified and named as plastid targeted protein (*CpPTP*). The ability of *CpPTP* to interact with DNA and its localisation in chloroplasts during dehydration suggests the importance of this protein in remodelling and/or protecting the chloroplasts from dehydration induced damage [62].

6. Role of ROS

During dehydration stress the production of ROS is increased in plant tissues. Generation of ROS is an indispensable process for all aerobic organisms. Every living aerobic cell relies on a dynamic balance between ROS production and ROS utilization under optimal growth conditions. The rapid increase in ROS levels is defined as "oxidative burst" [162,163]. The production and removal of ROS must be strictly controlled in order to maintain a redox balance. The equilibrium between production and scavenging of ROS may be perturbed by a number of adverse abiotic stress factors such as high light, drought, low temperature, high temperature, and mechanical stress [145,164–166]. Also desiccation triggers an increased production of ROS such as O_2^- radical and H_2O_2 [167]. The metabolism associated with photosynthesis and respiration is particularly sensitive to free radical production under water stress [109,110]. Traditionally ROS were considered to be toxic byproducts of aerobic metabolism which were disposed of by antioxidants, but several reports are available suggesting the importance of ROS as signaling molecules to control processes such as programmed cell death, abiotic stress responses, pathogen defense and systemic signaling [163,168,169].

7. Generation of ROS

In plant cells, ROS are produced predominantly in chloroplasts, mitochondria, and peroxisomes [145,170,171] as byproducts of various metabolic pathways [166,172]. In photosynthesizing green leaves, the major source of ROS comes from at least three distinct processes. First among these processes is the light-mediated over excitation of chlorophyll leading to ROS generation at PS II [145,173,174]. A second process involves the Mehler reaction at PS I in which O_2 is reduced to O_2^- radical directly by photosynthetic electron transport [175–177]. Finally in photorespiration, the recycling of phosphoglycolate formed by the oxygenase reaction of Rubisco leads to substantial production of H_2O_2 by a peroxisome-located glycolate oxidase [178,179]. Under conditions that impair CO_2 fixation in chloroplasts, the oxygenase activity of ribulose-1,5-bisphosphate carboxylase/oxygenase increases and the produced glycolate is transported to peroxisomes, where it is oxidized by glycolate oxidase forming H_2O_2. Even during optimal physiological conditions, a small portion of the total O_2 is converted to ROS [175].

The mitochondrial electron transport chain is another major site for the generation of ROS such as superoxide and H_2O_2, which is referred to as mitochondrial ROS (mROS) [180]. The estimated H_2O_2 production in mitochondria may be 20 times lower than in the chloroplasts, at least in C_3 plants [181]. Although mROS production is much lower compared to chloroplasts, mROS are important regulators of a number of cellular processes including stress adaptation and programmed cell death [169]. Mitochondrial electron transport chain (ETC) complexes I and III probably represent the primary sites of mROS generation. While the relative importance of these two sites for mROS generation and the factors influencing their rates of mROS production are largely unknown, an important generalization is that mROS formation increases as the ETC becomes more highly reduced [182]. There is hardly any information on the generation on mitochondrial ROS in resurrection plants. Tuba et al. [137] have suggested that photosynthesis is more susceptible than respiration to oxidative damage, since the continuation of respiration is necessary to provide energy for the acquisition of sub-cellular protection.

8. ROS avoidance/protection in resurrection plants

During desiccation in the presence of light, singlet oxygen radicals are actively produced by the transfer of excitation energy from chlorophyll molecules to oxygen initiating the free radical generating process and formation of ROS [109,183,184] but oxidative damage is effectively prevented in resurrection plants. The formation of superoxide and hydroxyl radicals results in the damage of essential cellular components such as nucleic acids, polysaccharides, proteins and membrane lipids [185]. To prevent damage associated with oxidative stress resurrection plants have evolved various protective mechanisms [9,10]. Resurrection plants upregulate synthesis of various antioxidants [14,28]. These pigments act as sun-screen by masking the chlorophyll from excessive radiation [14,22]. *C. wilmsii* and *M. flabellifolia* which retain most of their chlorophyll during drying minimize photo-oxidation by chlorophyll shading through leaf folding, antioxidant protection in the form of enzyme activity and anthocyanin accumulation along with shutting down photosynthesis [28]. In *R. serbica*, phenolic acids are accumulated for the detoxification of hydrogen peroxide produced during dehydration [186]. It has been reported that lutein the most abundant xanthophyll in the photosynthetic apparatus of higher plants has the specific property of quenching chlorophyll triplets by binding at the L1 site of the major LHCII complex thereby preventing ROS formation [187]. Poikilochlorophyllous resurrection plants such as *Xerophyta* species avoid free radical formation caused by energy transfer from excited chlorophyll to oxygen [24,144]. This strategy has the disadvantage that the photosynthetic system has to be resynthesized *de novo* upon rehydration which delays recovery. Since the chlorophyll is retained and the

photosynthetic apparatus is perfectly maintained in desiccated state, homoiochlorophyllous plants need better antioxidant protection against free radical attack than poikilochlorophyllous plants [188]. The down-regulation of photosynthesis can avoid photooxidation by energy dissipation. One of the mechanisms suggested to be involved in this protection is energy dissipation via the carotenoids of the xanthophyll cycle (zeaxanthin, antheraxanthin and violaxanthin) [189]. During desiccation the substantial increase in zeaxanthin content was observed in *C. plantagineum* [140] and *H. rhodopensis* [150]. In *B. hygrometrica* upon desiccation an increase in carotenoid content was observed which implicates the protection of photosynthetic apparatus by the xanthophyll cycle [127,190].

9. Antioxidant defense mechanisms

Plants induce antioxidant defense systems in response to ROS to diminish cytotoxic damage such as lipid peroxidation, protein modification and DNA damage [146,191,192]. These defense strategies are not only restricted to the intracellular compartments, but are also found in the apoplast to a limited extent [168,193]. Higher plants contain numerous enzymatic, non-enzymatic ROS-scavengers and both water and lipid soluble antioxidants localized in different cellular compartments [175,191,194]. The enzymatic ROS scavenging system consists of several enzymes like superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDAR), dehydroascorbate reductase (DHAR), glutathione peroxidase (GPX), and glutathione reductase (GR). Non-enzymatic antioxidants include pigments, tripeptide thiol (glutathione), ascorbate (vitamin C), α-tocopherol (vitamin E) and others. These are considered as general 'housekeeping' protectants because they are not unique to resurrection plants [14,61].

Within the cell, SODs constitute the first line of defense against ROS. SOD, the family of metallo-enzymes catalyzes the disproportionation of superoxide (O_2^-) to molecular oxygen and H_2O_2. SOD removes superoxide and hence decreases the risk of hydroxyl radical formation from superoxide via the metal-catalyzed Haber–Weiss type reaction. Based on the metal co-factor used by the enzyme, SODs are classified into three groups (Mn-SOD, Fe-SOD and Cu/Zn-SOD) located in three different compartments of the cell. All the three groups play a key role in protection against oxidative stress [195,196]. Mn-SOD is predominantly found in mitochondria and peroxisomes, Fe-SOD is located in the chloroplast and Cu/Zn-SOD is located in the chloroplast, cytosol and possibly in the extracellular space [197].

Monofunctional, tetrameric and heme-containing catalases are mostly localized in peroxisomes or glyoxysomes [198–200]. CAT itself is inhibited by ROS, such as O_2^- [201] and is generally inactivated by UV or visible light in the presence of O_2. The ascorbate-glutathione (Asc-GSH) cycle that occurs in chloroplasts, cytoplasm, and mitochondria [194] has also been demonstrated in peroxisomes [170,202]. This cycle is catalyzed by a set of four enzymes, APX, monodehydroascorbate reductase (MDAR), glutathione-dependent dehydroascorbate reductase (DHAR), and glutathione reductase (GR). The primary peroxidation of ascorbate by APX yields the monodehydroascorbate (MDA) radical that is either directly reduced back to ascorbate by MDAR [203] or undergoes non-enzymatic disproportionation to ascorbate and dehydroascorbate. Recovery of the ascorbate from dehydroascorbate occurs via the glutathione-dependent reaction catalyzed by DHAR, and the oxidized glutathione dimers are re-reduced by the NADPH-dependent GR [204]. Tocopherol, ascorbate and glutathione are central components of plant antioxidant defences combatting together to limiting ROS accumulation [205]. Mutants with decreased ascorbate levels or altered glutathione content are hypersensitive to stress [206,207]. Glutathione (GSH) is oxidized by ROS, forming oxidized glutathione (GSSG) and ascorbate is oxidized to monodehydroascorbate (MDA) and dehydroascorbate (DHA) through the Asc-GSH cycle. GSSG, MDA, and DHA can be reduced reforming GSH and ascorbate.

10. Antioxidants in resurrection plants

A substantial increase in total SOD levels in *R. serbica* leaves is observed upon dehydration thereby indicating the role of antioxidant defense during desiccation in resurrection plants. Mn-SOD and Fe-SOD levels increased during dehydration in these plants whereas Cu/Zn SOD is not detected [208]. Increased activities of APX and GR have been reported during dehydration in several resurrection plants [14,28,208,209]. Increased activities of SOD, APX and CAT were also observed in *Selaginella bryopteris*, a lycophytic resurrection plant, upon desiccation [210]. The importance of the antioxidant status for the revival of the resurrection plant, *M. flabellifolia* and conferring desiccation tolerance has been described by Kranner et al. [188]. In this homoiochlorophyllous resurrection plant, which retains high concentrations of chlorophyll during dehydration, the accumulation of antioxidants like ascorbate, glutathione and α-tocopherol are observed upon dehydration. The increases in antioxidants upon rehydration were only observed in vegetative tissues desiccated for 4 months. The oxidative damage to the vegetative tissues increased with the duration of desiccation. Upon rehydration the formation of ascorbate and glutathione (GSH) is observed by simultaneous reduction of their oxidised forms (DHA and GSSG). Plants that have been desiccated for a long time more than 8 months were unable to rehydrate which was correlated with the depletion of antioxidants [188]. This demonstrates the importance of the antioxidant systems for the recovery.

Several members of the aldehyde dehydrogenase (ALDH) family which play an important role in detoxifying aldehydes generated during desiccation have been identified in both seeds and the dehydrated vegetative tissues of resurrection plants [211]. Apart from this the peroxiredoxins which belong to the class of conserved thiol-specific antioxidant enzymes are also increased during desiccation in resurrection plants [86,212–214]. A new desiccation inducible antioxidant enzyme corresponding to a form of 1-cys peroxiredoxin, was identified in the leaves of *X. viscosa* which shows more than 70% sequence identity to seed-specific 1-cys peroxiredoxins and it is the only 1-cys peroxiredoxin that has been reported in vegetative tissues [213,215–218]. Its transcript is absent in fully hydrated leaves, but it accumulates upon dehydration and upon other stresses that lead to increased levels of ROS [213]. Interestingly, 1-cys peroxiredoxin is not expressed only during dehydration but also during rehydration in *T. ruralis* [7]. The nuclear location of this peroxiredoxin points to an involvement of this protein in protecting the nuclear compartment from ROS [213]. BLAST analysis of the transcript contigs of *C. plantagineum* with other plant species revealed a closer relationship with *Vitis vinifera*, *Ricinus communis* and *Populus trichocarpa* than to the model plant *Arabidopsis*. Transcriptome analysis shown in Rodriguez et al. [115] confirmed the differential expression of transcripts encoding proteins involved in desiccation tolerance as described earlier in different articles [96,160,211,106]. Out of these, the proteins protective against oxidative stress and enzymes involved in the metabolism of vitamin-K are highly abundant in rehydrated plant tissues and interestingly significant increase in transcripts related to thiamine metabolism was observed in dehydrated samples assumed to protect from oxidative stress [115].

11. Conclusions and outlook

To summarize, the resurrection plants are endowed with various protective mechanisms to combat desiccation, while some

responses are inductive others are being constitutive. Unique changes in chloroplast structure, thylakoid membrane integrity, photochemical activities and protection against oxidative stress by antioxidative systems during desiccation and rehydration cycles make these plants model systems to explore the novel genes and metabolites involved in desiccation tolerance. The accumulated physiological, biochemical and molecular data based on the technological advancements made by using various 'omics' techniques such as transcriptomics and proteomics advanced our understanding of desiccation tolerance. Although considerable progress has been made in understanding the desiccation tolerance in resurrection plants, there are still different aspects which require attention. Decrease in the photosynthesis during dehydration is the only common phenomenon which is observed in all plants undergoing dehydration. In many instances species-specific responses contributing to the revival of photosynthesis were discussed. The photosynthetic apparatus in homoiochlorophyllous plants and poikilochlorophyllous plants has been well studied and information is available on the loss or retainment of chlorophyll. However, how photosynthesis recovers following dehydration is still an open question. It would be interesting to study the regulation of Rubisco activase in resurrection plants, since it is an important enzyme required for Rubisco activity thereby for the restoration of photosynthesis during rehydration. Multilevel genomic studies overlapping with physiological and biochemical studies are necessary to unravel the hidden mechanisms allowing full recovery of photosynthesis. Since the tolerance to desiccation requires the thylakoid membranes to withstand mechanical stress, studies are needed on membranes focusing on the identification of factors that contribute to membrane stability. Recently, *SENSITIVE TO FREEZING 2* (*SFR2*) gene encoding a galactolipid remodelling enzyme of the outer chloroplast envelope membrane is reported to be involved in the stabilization of membranes leading to freezing tolerance in *Arabidopsis* [219]. The dual nature of ROS suggests that it can be utilised as an environmental indicator and biological signal. ROS acting as a secondary messenger and modulating the activities of specific target molecules involved in signaling and transcription in *Arabidopsis* is known but the role of ROS in resurrection plants has still to be explored.

Acknowledgement

D.B. and D.D. are members of the EU COST action FA0605 INPAS which inspired this review.

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