Review

Towards a systems-based understanding of plant desiccation tolerance

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Vegetative desiccation tolerance occurs in a unique group of species termed 'resurrection plants'. Here, we review the molecular genetic, physiological, biochemical, ultrastructural and biophysical studies that have been performed on a variety of resurrection plants to discover the mechanisms responsible for their tolerance. Desiccation tolerance in resurrection plants involves a combination of molecular genetic mechanisms, metabolic and antioxidant systems as well as macromolecular and structural stabilizing processes. We propose that a systems-biology approach coupled with multivariate data analysis is best suited to unraveling the mechanisms responsible for plant desiccation tolerance, as well as their integration with one another. This is of particular relevance to molecular biological engineering strategies for improving plant drought tolerance in important crop species, such as maize (*Zea mays*) and grapevine (*Vitis vinifera*).

We dedicate this manuscript to our colleague, the late Professor George G. Lindsey.

Desiccation tolerance in resurrection plants

The phenomenon of desiccation tolerance is found throughout the microbial, fungal, animal and plant kingdoms [1,2]. In the plant kingdom, it is mainly seeds and non-tracheophytes, such as mosses, that commonly display tolerance to desiccation [3]. Desiccation tolerance, as opposed to drought tolerance, which involves surviving moderate water loss (e.g. 90% relative water content [RWC]), is the ability to survive absolute water contents of 0.1 g H_2O g^{-1} [2]. Most seeds are termed 'orthodox' because they can survive dehydration to an air-dry state, whereas a minority is called 'recalcitrant' because they show a marked sensitivity to such severe dehydration [4]. Many mosses, lichens and ferns can survive dehydration of their vegetative organs (e.g. leaves), whereas this is uncommon in tracheophytes [3,5,6]. Although there are no gymnosperms that show vegetative desiccation tolerance, there are several angiosperm families that contain desiccation-tolerant members [3]. These individual species are collectively referred to as 'resurrection plants' [7]. Upon dehydration, resurrection plants shrivel up and fold their leaves until water is available, whereupon these plants revive in a remarkable manner (see Online Supplementary Movies showing resurrection plants rehydrating).

A rich diversity of resurrection plants is found in southern Africa, a region of significant arid and semi-arid areas [7]. Several species, including *Myrothamnus flabellifolia* [8], *Craterostigma plantagineum* [9], *Craterostigma wilmsii* [10], *Xerophyta viscosa* [11], *Xerophyta humilis* [12], *Eragrostis nindensis* [13] and *Sporobolus stapfianus* [14,15] (Figure 1), have been intensively studied with the goal of identifying the mechanisms responsible for their remarkable tolerance (Figure 1). Desiccation tolerance seems to not necessarily require the presence of novel molecular structures; however, the developmentally triggered re-activation of established pathways and processes seems to be crucial in conferring tolerance [2,9].

Research on desiccation tolerance has generally been conducted using discipline-specific approaches, focusing exclusively on the physiological [16,17], metabolic [15], molecular genetic [14,18], biochemical [19,20] or ultrastructural [21] changes that occur in resurrection plants during dehydration and rehydration. Although such research has been responsible for significant advances in our understanding of desiccation tolerance, discipline-specific approaches suffer because the process under study is inherently complex and requires cross-disciplinary investigations to link the various concepts related to tolerance into a coherent whole. Here, we present major recent advances made through studying a variety of different aspects that seem to be important for resurrection plants to be able to survive desiccation. These include gene regulation networks and signal transduction pathways [9,14], compatible solutes and carbohydrate metabolism [15,22], desiccation-associated proteins [19,23], conventional and novel antioxidants [20,24,25], membrane protectants [20] and cell wall properties [21,26–28]. We believe that, for tolerance to emerge, these fundamental processes, constituting cellular information regulation, energy metabolism and structural organization, must be inte-

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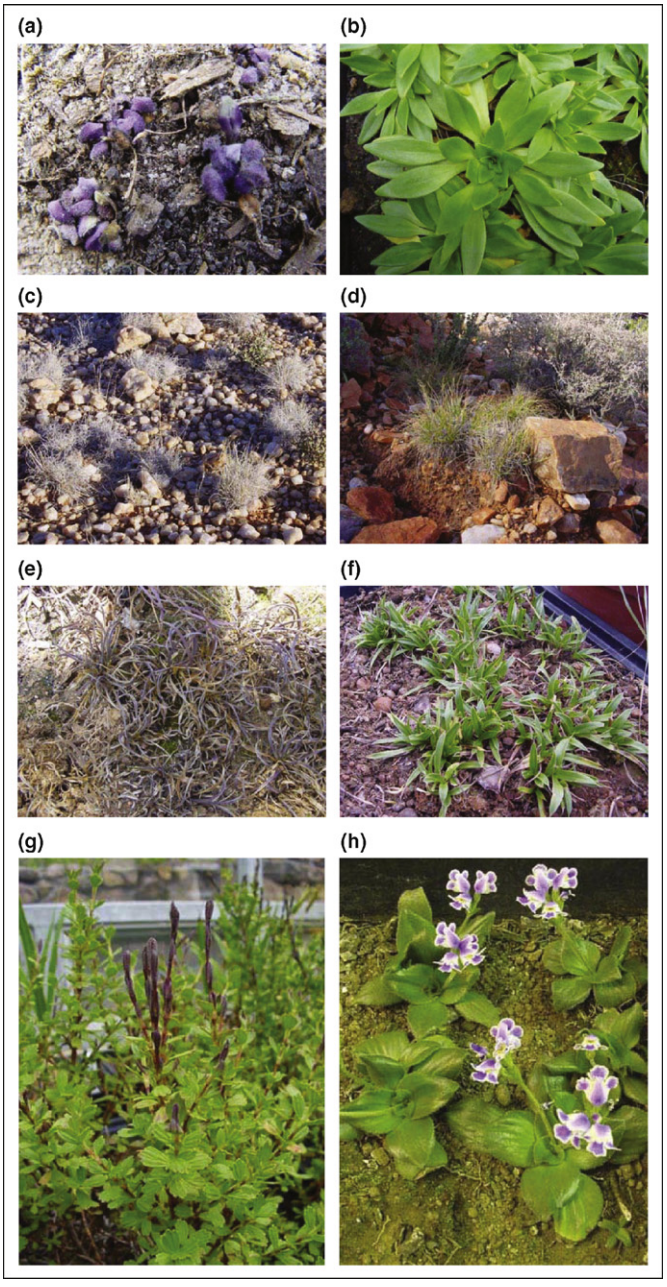

Figure 1. Examples of South African resurrection plants investigated to determine the mechanisms of desiccation tolerance. *Craterostigma wilmsii* dehydrated **(a)** and hydrated **(b)**; *Eragrostis nindensis* dehydrated **(c)** and hydrated **(d)**; *Xerophyta humilis* dehydrated **(e)** and hydrated **(f)**; partially rehydrated *Myrothamnus flabellifolia* **(g)**; and hydrated *Craterostigma plantagineum* **(h)**. Reproduced with permission from Jill Farrant.

grated through coordinated metabolic and signaling events. Furthermore, we propose that using a systems-biology approach will lead to a significantly improved understanding of the mechanisms associated with plant desiccation tolerance. This is important for improving the application of genetic-engineering approaches in enhancing drought tolerance in valuable crop species, such as maize (*Zea mays*) and grapevine (*Vitis vinifera*).

Signaling mechanisms, gene regulation and functional proteomics

Drought perception and regulatory networks

Knowledge of the regulatory networks controlling drought responses in plants has advanced tremendously during the past decade [29]. In contrast to model plants such as *Arabidopsis thaliana*, very little information is available on signaling pathways in resurrection plants. This scarcity of information might be a consequence of the fact that the molecular basis of desiccation tolerance has only been studied in relatively few species; namely, the lycopod *Selaginella lepidophylla* [30], the moss *Tortula ruralis* [31], the monocotyledons *S. stapfianus* [14], *X. viscosa* [11] and *X. humilis* [32], and the dicotyledons *C. plantagineum* [9] and *M. flabellifolia* [8]. For example, in *C. plantagineum*, the synthesis of phospholipid-based signaling molecules is one of the earliest events in the perception of water stress [33]. Phospholipase D (PLD) activity is induced within minutes by dehydration stress, but not by abscisic acid (ABA), a known signaling molecule involved in desiccation tolerance [33]. The constitutively expressed *CpPLD-1* (AJ133001) transcript is thought to be involved in early responses to dehydration by producing second messenger molecules, whereas the dehydration-induced *CpPLD-2* (AJ133000) might be involved in phospholipid metabolism [33]; *CpPLD-1* and *CpPLD-2* both encode phospholipases.

In comparison to early perception events, more is now known about downstream processes of the dehydration response signaling pathway in resurrection plants. Genes that are expressed in response to drought stress in resurrection plants are classified into two main types: (i) those such as transcription factors and regulatory RNAs, which control the expression of other genes, and (ii) those that encode products with putative protective functions.

Several classes of drought-induced transcription factors have been isolated from *C. plantagineum*; namely, the myeloblastosis (MYB) family [34], homeodomain-leucine zipper (HD-Zip) family [35,36], basic leucine zipper domain (bZIP) family [37] and a novel zinc finger [38]. Two Myb-related genes, *CpMyb7* and C*pMyb10* (AF510112), show differential expression and regulation in response to desiccation and to ABA in different tissues of *C. plantagineum* [34]. Interestingly, transgenic *A. thaliana* plants overexpressing C*pMyb10* displayed increased tolerance to drought and salt stress [39]. Several drought-regulated HD-Zip genes have also been isolated from *C. plantagineum*, with some being inducible by both dehydration and exogenously applied ABA. In both desiccation-tolerant and desiccation-sensitive plants, the expression of drought-responsive genes is mediated by ABA-independent and -dependent signal transduction pathways. Transgenic tobacco (*Nicotiana tabacum*) and *A. thaliana* plants that ectopically express the HD-Zip transcription factor *CpHB-7* (AF44223623) display reduced sensitivity towards ABA during seed germination and stomatal closure [36]. The ABA- and dehydration-responsive dehydrin gene, *CDeT6-19*, has been identified as one of the potential target genes of CpHB-7 [36]. In addition, a bZIP transcription factor, CpbZIP1 (DQ073569), and three highly conserved histone H3 proteins have been shown to bind to the promoter of the dehydration-induced group 4 late embryogenesis abundant (LEA) gene, *CpC2* [37]. Although the exact function of CpbZIP1 is unknown, a repressor function, possibly by inhibition of other transcription factors from binding to the *CpC2* promoter, has been suggested [37].

Role of small regulatory RNA molecules

Research over the past few years has highlighted the significance of small RNAs in regulating plant responses to abiotic stress [40]. Overexpression of *CRATEROSTIGMA DESICCATION TOLERANT-1* (*CDT-1*; AJ250122), a dehydration- and ABA-inducible gene, resulted in constitutive expression of dehydration- and ABA-responsive transcripts and contributed to desiccation tolerance of *C. plantagineum* callus tissue in the absence of ABA treatment. *CDT-1* and other functionally related gene members [41] have features of short interspersed retrotransposon elements and are hypothesized to act as regulatory noncoding RNA molecules [41]. It was recently shown that translation of the *CDT-1* transcript is not required for the induction of desiccation tolerance because *C. plantagineum* calli transformed with mutated versions of the *CDT-1* gene are constitutively desiccation-tolerant [42]. *CDT-1* does have the ability to encode a small interfering RNA (siRNA) and can induce desiccation tolerance in callus tissue of *C. plantagineum* [42]. This suggests that retrotransposons and siRNA have a role in the evolution of desiccation tolerance in *C. plantagineum*. Currently, *CDT-1* and its closely related gene members seem to be unique to *C. plantagineum* [41]. However, it is likely that more regulatory RNAs involved in desiccation tolerance will be discovered because evidence is accumulating that gene regulation by small RNAs is a common mechanism in plant stress response pathways [40].

Transcriptomic and proteomic studies

Transcriptomic approaches have identified many mRNAs that are induced by dehydration, whereas corresponding information on the proteomes of resurrection plants is limited. A two-dimensional (2D) SDS–PAGE analysis of the *S. stapfianus* leaf demonstrated that the protein complement changes during the induction of desiccation tolerance [43]. 2D SDS–PAGE was also used to study *de novo* protein synthesis during rehydration in *T. ruralis* [44] and *C. plantagineum* [45]. However, in these studies, limited data were presented on the identification and assignment of protein bands. Recently, changes in the leaf proteomes of resurrection plants during desiccation were examined in *X. viscosa* [46] and *Boea hygrometrica* [47]. In detached *B. hygrometrica* leaf tissue, dehydration-induced proteins include an ABC transporter and a vacuolar H^+-ATPase that might be involved in protection against osmotic stress, a glutathione peroxidase-like protein that might be involved in oxidative stress protection and a polyphenol oxidase that might prevent proteolytic activity [47]. In severely dehydrated *X. viscosa* leaf tissue (35% relative leaf water content), proteins that increase in abundance include a chloroplast FtsH protease, GDP-mannose-3′,5′-epimerase, alcohol dehydrogenase, protein phosphatase type 2C and 2-cys peroxiredoxin [46]. Of particular interest are proteins synthesized *de novo* upon dehydration. These include a dnaK-type molecular chaperone, RNA-binding protein, phosphopyruvate hydratase and a desiccation-related protein.

A major hindrance to proteomic analysis in resurrection plants is the lack of a large genomic or EST database. For both *X. viscosa* [46] and *B. hygrometrica* [47], this has resulted in low (~30%) success rates for protein identification. Although large EST collections (~10 000) are available for *T. ruralis* [48] and *X. humilis* [32], this number is probably still too low to increase the protein identification success rates needed for proteomic studies. A genome-sequencing initiative focusing on one or two model resurrection plant species (e.g. a dicotyledon such as *C. plantagineum* and a monocotyledon such as *X. humilis*) would be a tremendous step forward in supporting transcriptomic and proteomic studies of these plants.

Metabolic adjustment and antioxidant systems

Many mRNAs and proteins identified in resurrection plants undergoing re-/dehydration are involved in photosynthesis and carbohydrate metabolism. Plant metabolic processes such as photosynthesis and carbohydrate metabolism are sensitive to water deficit [16,49]. Resurrection plants can protect their photosynthetic apparatus and modify their metabolism in response to desiccation [15,50]. Homoiochlorophyllous resurrection plants, such as *M. flabellifolia*, retain their chlorophyll when dehydrated [8], whereas poikilochlorophyllous resurrection plants degrade their chlorophyll and resynthesize it after rehydration [16]. Homoiochlorophylly carries a greater risk of photo-oxidative and metabolic damage occurring because active photosystems can be uncoupled from metabolic dissipation mechanisms, resulting in oxidative damage. To protect against such damage, these plants contain antioxidant enzymes such as superoxide dismutase, glutathione reductase and ascorbate peroxidase, which are considered to be general 'housekeeping' protectants because they are not unique to resurrection plants [12,25]. Several members of the aldehyde dehydrogenase (ALDH) family have been identified in both seeds and in dehydrated vegetative tissues of resurrection plants [51,52]. It was demonstrated that mRNA and protein levels of GAPDHc, a member of the ALDH11 (GAPDH) (AY504666) family, increased in response to desiccation in the leaves of *C. plantagineum* [51]. Furthermore, the ABA- and dehydration-induced Cp-ALDH protein can oxidize toxic nonanal, propionaldehyde and acetaldehyde [52]. In *T. ruralis,* the *ALDH21A1* gene (AI305018) is thought to have an important role in the detoxification of aldehydes generated in response to desiccation and salinity stress [53]. Another antioxidant enzyme, the seed-specific 1-cys-peroxiredoxin, has been previously shown to be abundantly expressed during desiccation in the leaves of *X. humilis* and *X. viscosa* [11]. Interestingly, a 1-cys peroxiredoxin is also expressed during not only dehydration but also rehydration of *T. ruralis* [54].

The importance of antioxidant systems in desiccation tolerance has been highlighted by a recent study on *M. flabellifolia* [24]. The classical Haliwell-Asada antioxidant pathway was shown to be compromised in *M. flabellifolia* plants that had been desiccated for unnaturally long periods (>9 months) [24]. In addition, antioxidants, such as polyphenols (galloylquinic acids) were shown to correlate with the period (9 months in South Africa, 2–3 years in Namibia) for which different *M. flabellifolia* populations can remain desiccated [20,55]. These chemical antioxidants might act as a 'reservoir' and determine the period

for which a plant can remain desiccated before its viability is compromised [20,55]. Support for the antioxidant role of polyphenols and phenolic antioxidant enzymes has been gained from studies on the European resurrection plant *Ramonda serbica* [56–58]. Conventional and novel antioxidant enzymes, such as superoxidase [57] and polyphenol oxidase [58], respectively, were shown to be upregulated in response to desiccation. Similar correlations were also found for phenolic acids [56], lending support to their hypothesized antioxidant function in desiccation tolerance.

Carbohydrate metabolism and compatible solutes

In addition to antioxidant metabolism, normal carbohydrate metabolism is re-routed in resurrection plants undergoing dehydration [51]. Accumulation of sucrose [59] and trehalose [60], as well as short-chain oligosaccharides such as raffinose [22], is observed in dehydrating resurrection plants. Enzymes of central carbohydrate metabolism, such as sucrose phosphate synthase [15,61] and hexokinase [59], are activated upon desiccation, which results in a re-direction of carbon flow from reserve substances (e.g. starch or octulose [62]) to soluble saccharides such as sucrose. Amino acid metabolism is also modified during desiccation [15], and it is known that compatible solutes, such as proline, accumulate during dehydration [63]. Saccharides such as sucrose are known membrane protectants and can stabilize cellular processes [63]. Recently, it has been shown that glucose and sucrose accumulate in specific locations in resurrection plant tissue during dehydration and probably function to protect specific cellular structures (e.g. chloroplasts and tonoplast membranes) from desiccation [64].

Macromolecular and mechanical stability

The dehydration-induced accumulation of structure-stabilizing molecules, such as the LEA proteins [65,66], has been studied in several resurrection plants. Many of these LEA-protein-encoding genes are activated under moderate dehydration conditions (>65% relative water content) in both desiccation-sensitive and -tolerant tissues and are proposed to protect plants only at higher water contents [12]. LEA genes are thought to have a role in defense against moderate to severe water loss, such as that experienced by orthodox (desiccation-tolerant) seeds during maturation or by resurrection plants during desiccation [12].

Several protective functions have been predicted for LEA proteins, including roles in protecting DNA, stabilizing cytoskeletal filaments and acting as molecular chaperones [67]. Recently, it has been shown that LEA proteins can act synergistically with sugars, such as trehalose, to prevent protein aggregation during desiccation [19]. The expression of at least 16 different LEA genes is activated during desiccation in *X. humilis* leaves [32]. The concurrent induction of multiple LEA genes during dehydration suggests that these LEAs might interact to stabilize and protect other proteins and membranes or that different LEAs are specifically targeted to different organelles or cellular structures to exert their protective function. At least two LEA proteins, CDeT11-24 and CDeT6-19, are required to be phosphorylated *in vivo* during desiccation [45]. LEAs might also have a role in recovery during rehydration in *T. ruralis* [50]. It has been proposed that, in rehydrating *T. ruralis* gametophytes, LEA proteins stabilize membranes or function in the reconstitution of damaged membranes [31]. Structurally considered to be random coils, LEA proteins have been shown to form stabilizing structures in the vicinity of membranes [68]. They have also been shown to act as antiaggregants and can protect the proteomes of desiccation-tolerant organisms against water-loss-induced aggregation [69].

Beyond LEA proteins, new evidence has emerged for other molecules, such as small heat shock proteins (smHSPs) [70] and polyphenols (galloylquinic acids) [20], with LEA protein-like properties. These molecules have been shown to protect membranes against desiccation, suggesting the possible existence of other novel components with LEA-like functions in resurrection plants.

Whereas cell membranes have been well studied with respect to desiccation-induced damage, less is known about how the cell walls of resurrection plants respond to desiccation [27]. To date, only the cell walls of *C. wilmsii* and *M. flabellifolia*, have been intensively studied using biochemical, immunocytochemical and microscopical techniques [21,28,71] (Figure 2). These studies have revealed two different mechanisms for stabilizing wall structures to desiccation. In *C. wilmsii*, several inducible responses occur, such as calcium ion redistribution and xyloglucan modification, which enhance wall strength and flexibility [28,71]. Based on studies performed in *C. plantagineum* [26], expansins are also believed to be involved. In the case of *M. flabellifolia*, it seems that constitutive 'pectic plasticizers', in the form of pectin-associated arabinans and/or arabinogalactan proteins, are important in keeping the cell wall flexible during desiccation [21,72]. Biophysical studies on species of the resurrection grass genus Eragrostis have also implicated wall extensibility and flexibility in desiccation tolerance [73,74]. Although more research is needed, these cell wall studies have highlighted target genes (i.e. encoding expansins and xyloglucan- and pectin-modifying enzymes) that could be engineered for improving the drought tolerance of non-tolerant species [27].

Systems biology and engineering plants for desiccation tolerance

Much research performed on resurrection plants is carried out with the intention of using the knowledge obtained to engineer drought tolerance into agronomically valuable crops. More than 100 dehydration-induced genes from several resurrection plants have now been characterized [32], although few have been introduced into desiccation-sensitive plants and tested for improving drought tolerance (Table 1). Several studies involving the transformation of *C. plantagineum* genes (specifically regulatory genes, e.g. transcription factors) into *A. thaliana*, tobacco and desiccation-sensitive callus tissue of *C. plantagineum* have been performed (Table 1) with mixed results: some experiments have shown improved drought tolerance [37], whereas others have shown no differences [39] or unexpected side effects such as ABA insensitivity [34]. The stress-inducible production of an *A. thaliana* aldehyde dehydrogenase driven by the *C. plantagineum CpC2* pro-

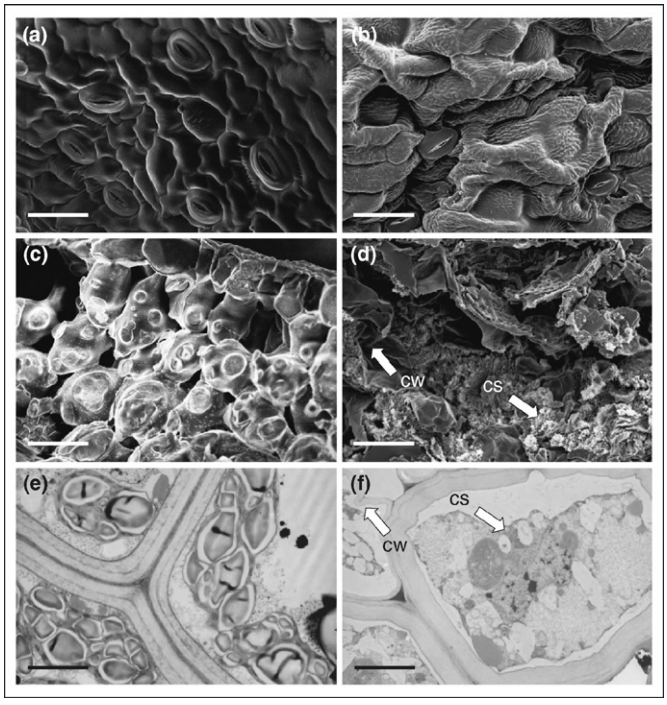

Figure 2. Ultrastructural changes associated with desiccation and rehydration in resurrection plants. Scanning electron micrographs of surface **(a,b)** and cross-sectional **(c,d)** views of hydrated (a,c) and desiccated (b,d) leaves of the woody resurrection plant *Myrothamnus flabellifolia*, showing leaf cell wall folding (CW) and cytosolic reorganization (CS). Transmission electron micrographs of hydrated **(e)** and dehydrated **(f)** leaf cells of the resurrection grass *Eragrostis nindensis*. Scale bars represent 30 μm (a–d) and 5 μm (e,f). Reproduced with permission from Jill Farrant.

moter in *A. thaliana* resulted in improved tolerance to oxidative and osmotic damage [75]. Recent experiments on transferring *X. viscosa* genes to *A. thaliana* have been carried out with promising results, including enhanced osmotolerance of transformed plants [76]. However, single-gene strategies, although useful for engineering specific traits such herbicide resistance, are significantly limited when attempting to produce as complex a characteristic as desiccation (or drought) tolerance.

A holistic approach is needed in which the most important genes involved in desiccation tolerance are engineered into sensitive species, thus allowing the coordinated expression of these genes to be observed. For this to be feasible, a modeling approach is necessary that identifies the key elements (e.g. genes, proteins and metabolites) of the plant metabolic network that are responsible for desiccation tolerance. Systems biology has emerged as a valuable approach for understanding the plethora of genetic, proteomic and metabolic processes that occur in living systems [77]. As opposed to assembling different biological pieces (as one would assemble a jigsaw puzzle), systems biologists attempt to understand the structure and dynamics of the organism under study [77]. It is necessary to understand how the individual parts function in the system before it is possible improve or repair existing systems. A systems-based understanding involves recognizing both system structures (e.g. gene interactions) and dynamics (e.g. metabolic fluxes). Furthermore, it is also important to understand how the system might be affected by external factors (e.g. water availability) and internal factors (developmental triggers) [77]. Thus it is necessary to simulate (using multivariate techniques) the system (e.g. resurrection plant or crop species) under study before modifications (e.g. using genetic techniques) can be made; this approach is termed the 'design method' and seeks to avoid the common practice of 'trial and error' in plant genetic engineering approaches [77].

Discovering the secrets of resurrection plants

Desiccation tolerance in resurrection plants is a multigenic and multi-factorial phenomenon. Here, we have highlighted the major research milestones achieved to date in understanding the various contributing systems, from gene regulation to metabolic and macromolecular stability. However, what is lacking is an understanding of how these individual factors 'interact' spatially and temporally. For example, are LEA proteins functionally redundant in the presence of saccharides? Which responses need to occur simultaneously (e.g. superoxide dismutase action and

Table 1. Transgenic plants engineered with resurrection plant genes and resultant phenotypes

Gene (Class)	Origin	Transgenic	Manipulation and phenotype	Refs
CpHB-7 (Homeodomain leucine zipper TF)	*Craterostigma plantagineum*	*Nicotiana tabacum*	Overexpression resulted in early germination and increased growth rate. Reduced ABA sensitivity during germination and stomatal closure was found. Transgenic plants show no differences in tolerance to drought or cold, but seeds show increased tolerance to salt stress	[36]
		Arabidopsis thaliana	Overexpression resulted in reduced ABA sensitivity during germination and stomatal closure	
CpMYB10 (Myb TF)	*C. plantagineum*	*A. thaliana*	Overexpression resulted in increased drought and salt tolerance. ABA hypersensitivity and glucose insensitivity during seed germination was observed	[39]
CDT-1 (Regulatory RNA)	*C. plantagineum*	*C. plantagineum*	Constitutive tissue-specific expression resulted in constitutive desiccation tolerance in callus tissue without ABA treatment	[41]
CpALDH stress-inducible CpC2 promoter fused to AtALDH311 (Aldehyde dehydrogenase)	*C. plantagineum*; *A. thaliana*	*A. thaliana*	Stress-inducible expression resulted in increased resistance to osmotic and oxidative stress. Protection against lipid peroxidation	[75]
XvSAP1 (Unknown)	*Xerophyta viscosa*	*A. thaliana*	Overexpression resulted in improved salinity, osmotic and high temperature stress tolerance	[76]

Abbreviations: ABA, abscisic acid; TF, transcription factor.

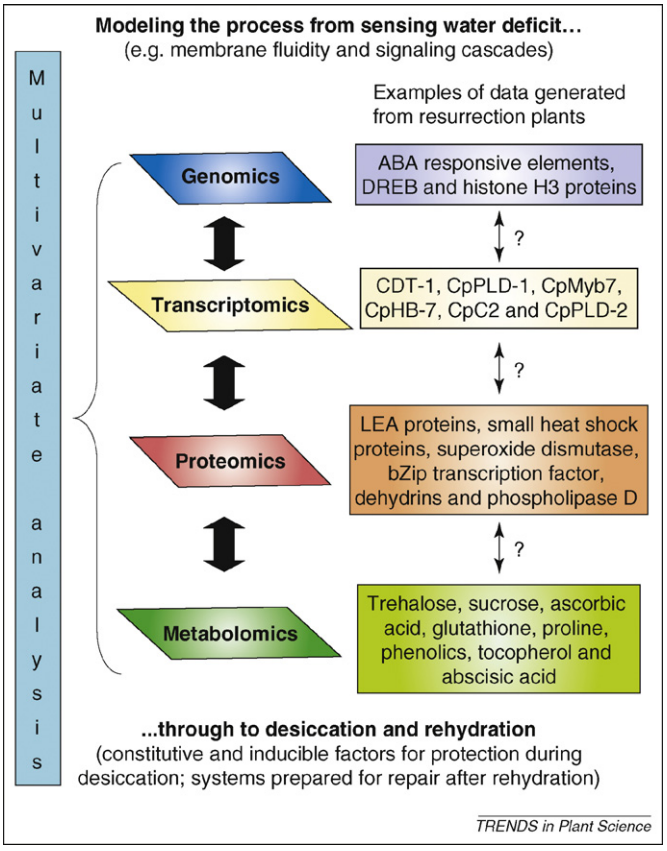

Figure 3. Using a systems-biology approach coupled with multivariate data analysis (chemometrics) to elucidate mechanisms responsible for desiccation tolerance in resurrection plants. Omics technologies (i.e. transcriptomics, proteomics and metabolomics) are used to generate datasets that need to be integrated through the use of multivariate statistics to understand the molecular processes from dehydration perception (at the cell membrane) to the emergence of a desiccation-tolerant phenotype. Examples of data generated from corresponding studies on resurrection plants (e.g. CDT-1 transcripts, LEA proteins and saccharide metabolites) are highlighted. Currently, the manner with which different datasets integrate (i.e. connect with each other) is not obvious (indicated by?). Chemometrics can be used to determine which of these factors are most important in contributing to desiccation tolerance. It is hoped that this multivariable approach will inform genetic engineering strategies to improve the drought tolerance of agronomically valuable crop plants.

ascorbic acid production) and in what order (e.g. first phospholipase activity followed by starch hydrolysis)? The difficulties in integrating these different systems into a coherent functional framework to elucidate the mechanisms responsible for plant desiccation tolerance need to be solved for progress to be made (see Figure 3 for a proposal to address this using systems biology). A limitation of using such an approach is that interesting and unique mechanisms, such as species-specific responses (e.g. phenolic production), might be overlooked, but this is outweighed by the advantage of discovering common mechanisms (i.e. system structures) and processes (i.e. system dynamics) that are crucial for desiccation tolerance. Coupling an evolutionary perspective to a systems-based approach to desiccation tolerance would significantly improve our understanding of which conserved mechanisms are crucial for surviving desiccation.

The application of '-omics' technologies, such as transcriptomics and proteomics, has begun to identify the catalogue of system components necessary for desiccation tolerance. In addition to the use of metabolomics technology in plant desiccation tolerance research, the application of chemometric and multivariate statistical modeling would be invaluable in assessing the degree to which various measurable factors (e.g. specific gene transcripts, proteins and metabolites) contribute to desiccation tolerance. Multivariate modeling would enable the integration of datasets (from genomic, transcriptomic, proteomic and metabolomic studies) and provide the tools for analyzing common trends and patterns. This would support the development of rational genetic engineering strategies, based on sound statistical data analysis and simulation modeling, for the improvement of drought tolerance in crop species. It is hoped that by following this combined approach, significant new insights into plant desiccation tolerance will be developed and new light will be shed on the seemingly miraculous nature of resurrection plants.

Supplementary data

Supplementary data associated with this article can be found at doi:10.1016/j.tplants.2008.11.007.

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