Desiccation Tolerance in Resurrection Plants

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To survive in the dry state, orthodox seeds acquire desiccation tolerance. As maturation progresses, the seeds gradually acquire longevity, which is the total timespan during which the dry seeds remain viable. The desiccation-tolerance mechanism(s) allow seeds to remain dry without losing their ability to germinate. This adaptive trait has played a key role in the evolution of land plants. Understanding the mechanisms for seed survival after desiccation is one of the central goals still unsolved. That is, the cellular protection during dry state and cell repair during rewatering involves a not entirely known molecular network(s).

orthodox seeds | Orthodox seeds | desiccation tolerance | resurrection plants | AGAMOUS- LIKE67 | peroxidase activity | cell wall folding | pectin esterification

1. Background

Although the core of desiccation-tolerance responses is retained in orthodox seeds, this special adaptation is only present in the vegetative organs of non-vascular plants (i.e., bryophytes) and few Angiosperm species (<0.15%; about 300 species) commonly known as resurrection plants [1][2][3][4]. That is, seeds and vegetative organs of resurrection plants are tolerant to desiccation and survive under water potentials of −100 MPa (i.e., 1–5% relative water content) and even lower [5][6]. Among other essential functions, resurrection plants resume photosynthetic activity and growth within a few hours after re-watering. Thus, a resurrection plant tolerates dehydration without affecting their vital attitudes. Phylogenetic evidence suggests that resurrection plants regained the ability to tolerate desiccation in their vegetative tissues through mechanisms present first in bryophytes [7]. Therefore, it is probable that almost all resurrection plants have reactivated in their vegetative parts the genetic specific program of orthodox seed desiccation tolerance [8]. In other words, presumably, the evolution of vegetative desiccation tolerance in resurrection plants occurred through co-option of the desiccation-tolerance mechanisms already active in seeds [1].

The regulatory interactions activating desiccation tolerance remain largely unknown. In order to control seed desiccation tolerance, the transcription factors (TFs) *PLATZ1* and *PLATZ2* (i.e., plant-specific zinc-dependent transcription repressors) and *AGL67* (i.e., AGAMOUS- LIKE67) act downstream of the embryo development regulatory master genes LAFL and are essential for the acquisition of desiccation tolerance in Arabidopsis seeds [9][10]. However, are these three genes conserved in Angiosperms? It is widely known that *LEC1* and *ABI3* are highly conserved from bryophytes to Angiosperms [10]. Interestingly, mutations in *LEC1*, *ABI3*, and *FUS3* drastically affect desiccation tolerance. On the other hand, the vegetative desiccation tolerance in the resurrection plant *Xerophyta*

humilis has not evolved through reactivation of the seed canonical LAFL network [11][12]. Transcriptome studies showed that the mechanisms involved in desiccation tolerance are conserved in resurrection plants, seeds, and pollen [13].

Together, investigating the mechanisms of desiccation tolerance in resurrection plants leads to understanding possible pathways for the evolution of desiccation tolerance in plants. To progress in this knowledge, the genomes of several species were recently sequenced and used as a model to understand the numerous interacting factors promoting desiccation tolerance. These studies include: (i) the lycophytes *Selaginella lepidophylla* [14] and *S. tamariscina* [15]; (ii) the monocots grass *Oropetium thomaeum* [16], and poikilochlorophyllous *Xerophyta viscosa* which destroyed the photosynthetic apparatus during dehydration and recovers it upon re-watering [17][8]; and (iii) the extremophile dicot *Boea hygrometrica* [18]. Genetic studies in *X. viscosa* are noteworthy since they have supplied valuable information on the genetic basis of desiccation tolerance [8]. These genomic advances provided profitable resources into the evolution of vascular plants and how resurrection plants acquired desiccation tolerance. In short, the molecular physiology and genomic and transcriptomic data from these model plants facilitate a wealth of information to study the conserved mechanisms of desiccation tolerance [4][15][19]). In dry viable seeds, almost all mRNAs are preserved as ribonucleoproteins to make them immediately available upon rehydration. However, it is not yet documented if resurrection plants use similar post-transcriptional and translational control mechanisms in prevision of rehydration.

2. Cell Wall Alterations

Desiccation tolerance is a convoluted multigenic and multifactorial process comprising a combination of structural and macromolecular changes, being the CW of the compartments involved. The CW is a highly dynamic cellular component [20], and its structure and composition are altered (i.e., remodeling) during cellular water loss [21]. Reactive xoygen species (ROS) are important molecules for the CW remodeling process given that they participate in compromised enzymatic reactions and work as signaling molecules [22][23]. Comparing the genomes of *Selaginella tamariscina* (desiccation tolerant) and *S. moellendorffii* (desiccation sensitive) demonstrated that the number of ROS-producing genes is much lower in the first lycophyte [15]. Interestingly, it was proposed that the ROS detoxification mechanisms within CW are less efficient than the intracellular ones because they rely on low levels of CW peroxidases [24]. In some resurrection plants, the peroxidase activities are highly increased upon re-watering but do not change during dehydration [25]. In *X. viscosa*, peroxidases are up-regulated during dehydration, but down-regulated upon rehydration, which is a prerequisite for CW stiffness under drought [26]. In other words, low peroxidase activities tend to generate hydroxyl radicals which lead to CW loosening. On the contrary, high amounts of peroxidases facilitate CW stiffness [27][28]. In parallel with these studies, screenings for foliar proteins interacting with dehydration induced CW proteins in resurrection of *C. plantagineum* identified a germin-like protein (CpGLP1). This CpGLP1 accumulates in the CW of desiccating leaves, binds with pectins, and has superoxide dismutase (SOD) activity [29]. The authors claim a role for this enzymatic activity in the ROS metabolism related to the control of CW plasticity during desiccation. It is noteworthy that the *OsGLP2-1* expression is increased in response to ABA and involved in the regulation of rice seed dormancy [30]. Interestingly, the balance between the

ABA and GA signals during seed germination is regulated by functional proteins such as *OsGLP2-1*, which bind to the promoters of *ABI5* and *GAMYB* [30].

Cell shrinkage, as water is lost, has negative effects on cellular structure and function. To adapt to this contraction stress, both the CW and plasmalemma fold, enabling maintenance of the membrane and the CW surface area, which is critical for cells to survive rehydration without breaking [31][32]. CW folding is a tightly regulated reorganization of the CW structure resulting in increased flexibility, allowing the CW to adjust to the reduced volume of desiccated cells more easily [33]. During the dehydration of *Craterostigma wilmsii*, a strong folding of CW takes place in foliar tissues, and a decrease of about 78% of the cell volume occurs. The CW folding is considered as an ability to maintain the contacts between the plasmalemma and the CW during dehydration and avoid the tearing between these structures, and hence cell lysis and death (see Table 2 from [4]). In later development, this stressful mechanical effect is minimized in both orthodox seeds and resurrection plants by CW folding and accumulation of dry matter to replace lost water. Therefore, unstructured LEA proteins, sugars, storage proteins, and simple polypeptides are accumulated [34]. These accumulated molecules likely also play a role in simple mechanical stabilization of desiccating cells [35]. In orthodox seeds, the large central vacuole fragments into multiple and more mechanically stable vacuoles, generally filled with storage proteins or compatible solutes. This vesiculation, which avoids the vacuole rupture, also occurs in resurrection plants. The vacuolar content can range from protein to metabolites and is heavily species dependent [17]. The folding process similarly occurs in both embryos and desiccating resurrection plants [36]. However, it is not clear whether the folding process and its regulation are similar in embryos and the leaves of resurrection plants subjected to dehydration. In resurrection plants, CW extensively shrinks and folds upon desiccation, but the integrity and continuity of CW structures are maintained and restored when tissues are re-watered [19][36].

The CW structural components were recently addressed in leaves of some resurrection plants [4][37]. Although the protective function of cellulose during water stress has been well studied, there is no information available about the relationship between cellulose and desiccation. However, high levels of de-methyl esterified homogalacturonan were found upon desiccation and the levels being reversed after re-watering. In *C. plantagineum* and *C. wilmsii*, xyloglucan and xylan, two cellulose-linking CW components, increased upon desiccation [37][38]. Likewise, in all studied resurrection plants, the changes in the pectin composition led to a more rigid CW upon dehydration [21]. De-methyl esterified pectin increases in the CW of *C. wilmsii*, *C. plantagineum*, and *L. brevidens*, which is probably due to pectin methyl esterase activities during dehydration [37]. In summary, desiccation-tolerant plants have an extraordinary ability to regrow when re-irrigated because they have an aptitude to alter the leaf structure, and modify both proteins and cellulosic and non-cellulosic polymers of CW. Finally, Table 1 from [21] summarizes the dehydration-induced changes in the expression of genes encoding proteins and enzymes that modify the CW in resurrection species. On the other hand, given that cellular turgency mechanically affects to CW, mechanosensors located in this structure detect alterations in the cell turgor [39]. Some of these sensors involved in dehydration were recently studied [40].

The transcriptome analysis in *C. plantagineum* revealed elevated expression of genes encoding pore Ca^{++} channels and others undefined upon dehydration [21]. Multi-omic analysis showed that several CW-related genes

involved in processes such as the regulation of CW plasticity, organization, and dynamics are differentially modulated upon dehydration. These analyses suggest the importance of CW remodeling during the acquisition of desiccation tolerance [41][42][43]. In conclusion, the activation in resurrection plants of metabolic routes leading to the increase in the flexibility of the CW structural components, as well as the increase in CW stability, suggests a tightly controlled folding process during dehydration that finally keeps the plasmalemma and photosynthetic apparatus intact. The study of these aspects in the seed will provide new reasons for understanding the process of tolerance to desiccation, a puzzle of enormous complexity.

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