Review

Mechanisms of seed desiccation tolerance and survival under dry conditions

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ABSTRACT

Desiccation tolerance is a critical adaptive trait that enables seeds to survive extreme dehydration and maintain viability during prolonged storage and unfavorable environmental conditions. This ability has been fundamental to plant evolution, contributing to successful reproduction, dispersal and long-term persistence of higher plants. In orthodox seeds, desiccation tolerance is acquired during seed maturation through coordinated physiological, biochemical and molecular processes, including dormancy induction, metabolic reprogramming and the accumulation of protective compounds such as late embryogenesis abundant (LEA) proteins, small heat-shock proteins, soluble sugars and antioxidants. These protective molecules stabilize cellular structures, prevent protein denaturation and aggregation and promote the formation of a cytoplasmic glassy state that preserves macromolecular integrity during dehydration. Hormonal regulation, particularly through abscisic acid (ABA) signaling and transcription factors such as ABI3 and ABI5, plays a central role in controlling these adaptive responses. Understanding the mechanisms underlying desiccation tolerance is essential for improving seed conservation strategies, enhancing crop resilience to environmental stress and supporting long-term germplasm preservation. This review summarizes the major physiological, biochemical and molecular mechanisms involved in seed desiccation tolerance and highlights their significance in seed biology and plant survival.

Keywords: Abscisic acid (ABA); ABI3; Cytoplasmic glass state; Desiccation tolerance; Late embryogenesis abundant (LEA) proteins; Orthodox seeds; Seed dormancy; Seed maturation; Soluble sugars; Vitrification

INTRODUCTION

One of the major challenges in long-term and large-scale seed conservation is the gradual physiological deterioration of seeds stored in gene banks (Chmielarz 2009). The nature of seeds, whether orthodox or recalcitrant, largely depends on their maturity at the time of shedding and species-specific characteristics (Barbedo 2018). Therefore, understanding seed physiological behaviour, particularly in relation to desiccation tolerance, is essential for obtaining high-quality seeds suitable for storage and conservation.

Desiccation is a natural developmental process occurring during the final stages of seed maturation, enabling seeds to enter a quiescent state and survive adverse environmental conditions (Dasgupta et al 1982, Beardmore and Whittle 2005). Desiccation tolerance (DT) refers to the capacity of seeds or plant tissues to survive extensive water loss and recover normal function upon rehydration. While most plants possess mechanisms to minimize water loss and maintain cellular water potential above that of the surrounding atmosphere, they generally remain sensitive to severe dehydration, with cellular water potentials between –3 and –6 MPa often proving lethal.

In contrast, desiccation-tolerant species can withstand much lower water potentials, sometimes reaching –100 MPa or below, allowing their cellular water status to equilibrate with ambient air without sustaining irreversible damage (Alpert and Oliver 2002). This remarkable ability is also observed in many seeds,

pollen grains and spores. The acquisition of desiccation tolerance typically coincides with the reserve accumulation phase that occurs prior to maturation drying. This process involves a range of metabolic and cellular adjustments essential for seed survival under dehydrated conditions.

According to Berjak and Pammenter (1999) and Oliver et al (2000), these adaptations include reduced vacuolation, intracellular dedifferentiation, lowered metabolic activity, accumulation of oleosins and free-radical scavengers and activation of repair mechanisms during rehydration.

Additionally, several protective compounds are believed to play critical roles in maintaining cellular stability during dehydration, including soluble sugars and cyclitols (Koster and Leopold 1988, Crowe et al 1992, Centeno et al 2016), amphipathic molecules (Hoekstra et al 1997) and late embryogenesis abundant (LEA) proteins (Kermode 1997, Wolkers et al 2001). Recent transcriptomic and proteomic studies have further confirmed the importance of these protective substances in the development of desiccation tolerance in orthodox seeds (Giarola et al 2017).

Seed desiccation is now recognized as a highly dynamic and metabolically active process involving significant changes in gene expression and biochemical pathways (Angelovici et al 2010). However, studying the mechanisms underlying desiccation tolerance remains challenging because these processes often overlap with normal developmental events during seed maturation (Farrant et al 2012). Before dehydration begins, seeds undergo substantial metabolic changes associated with nutrient uptake and reserve synthesis (Borisjuk et al 2004).

This developmental stage is characterized by active cell expansion, sucrose accumulation, increased energy availability and enhanced metabolic flux towards the production of storage compounds (Weber et al 2005). At the metabolic level, reserve accumulation is also associated with low-oxygen conditions that temporarily stimulate fermentative metabolism (Rolletschek et al 2004).

Together, these coordinated physiological and biochemical processes contribute to the successful acquisition of desiccation tolerance and ensure seed viability during storage and germination.

Dormancy and drying: two key traits along seed evolution

The emergence and persistence of plant life on land represent one of the most important milestones in earth's evolutionary history (Harrison 2017). This transition involved several major evolutionary advancements, including the development of a diploid sporophyte generation, a shift from gametophyte dominance to sporophyte dominance and the formation of specialized organs and tissues such as roots, leaves, vascular tissues, stomata, flowers and seeds (Ishizaki 2017).

Among these innovations, the ability of higher plants to produce seeds and other propagules has been fundamental to their reproductive success, dispersal and long-term survival. Over evolutionary time, seeds have undergone significant morphological and physiological adaptations that have enhanced their capacity to withstand diverse environmental conditions (Bareke 2018, Matilla 2019).

Seed development begins after fertilization and involves a series of coordinated events leading to the formation of three major components: the embryo, endosperm and seed coat. These structures develop together to produce a mature seed that is metabolically inactive, developmentally arrested and highly dehydrated (Penfield and MacGregor 2017).

This dormant condition serves as an adaptive mechanism that prevents germination under unfavorable conditions, thereby, ensuring that germination occurs only when environmental conditions are suitable for successful seedling establishment. Both internal physiological signals and external environmental factors regulate the induction and release of seed dormancy (Nonogaki 2019).

Dormancy can be described as a reversible state of reduced metabolic activity that allows organisms to survive periods of environmental stress. It plays a critical role in enabling organisms to withstand harsh conditions such as limited energy availability, temperature extremes, pressure variations and other biotic and abiotic challenges that fluctuate over time and space (Lennon and Jones 2011). In plants, seed dormancy allows survival across both temporal and spatial dimensions, making it a major evolutionary adaptation acquired during seed maturation (Agrawal et al 2021).

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Following substantial water loss during the desiccation process, seeds enter a dormant state that enables long-term survival. Similar to other anhydrobiotic organisms, seeds establish dormancy by transforming their cytoplasm into a metastable 'glass state,' where compatible osmolytes replace much of the cellular water. This structural reorganization helps stabilize cellular components and protects them from damage during dehydration.

However, not all seed tissues experience the same degree of water loss. Sensitive structures, particularly the embryo, require specialized protective mechanisms to prevent irreversible desiccation damage.

Several molecular and biochemical pathways contribute to protecting the embryo during seed drying. These include genes involved in the abscisic acid (ABA) signaling pathway, such as ABI3, as well as small heat-shock proteins (sHSPs) and late embryogenesis abundant (LEA) proteins, all of which play essential roles in maintaining cellular integrity during dehydration (Delahaie et al 2013).

ABA has been shown to regulate the accumulation of LEA proteins, thereby, enhancing the desiccation tolerance of developing seeds and improving their ability to survive under unfavorable environmental conditions (Tian et al 2020). Together, these adaptive mechanisms ensure seed viability, persistence and successful germination when favorable conditions return.

Seed desiccation tolerance: a trait to colonize terrestrial ecosystems

Desiccation tolerance refers to the ability of an organism or tissue to lose water until it reaches equilibrium with moderately dry air (typically 50% or lower relative humidity) and subsequently resume normal metabolic activity upon rehydration (Alpert 2005).

This remarkable characteristic can occur throughout the entire life cycle of some organisms or may be limited to specific structures within the same organism. For example, in many flowering plants, seeds possess strong desiccation tolerance, whereas, the sporophytic tissues rarely exhibit this capability.

Desiccation tolerance is also found across a wide range of phylogenetically unrelated organisms, including fungi, mosses, ferns and even certain invertebrates such as tardigrades, highlighting its broad evolutionary significance (Gechev et al 2013).

The ability to tolerate extreme water loss is considered an essential adaptation that enabled primitive plants to successfully colonize terrestrial environments. The molecular and physiological mechanisms underlying desiccation tolerance are believed to be ancient and have been largely conserved throughout plant evolution, particularly in angiosperms. However, for desiccation tolerance to be effective, any cellular damage caused by severe dehydration must be reversible upon rehydration (Oliver et al 2020).

To survive the mechanical and physiological stresses associated with dehydration, desiccation-tolerant cells employ various protective strategies. These include enhanced vacuolation and cell wall folding, which help reduce structural damage caused by water loss and maintain cellular integrity during drying (Chen et al 2020). Such adaptations enable cells to withstand significant fluctuations in hydration while preserving essential biological functions.

In contrast, most plants, particularly agricultural crops categorized as drought-avoiding species, have limited capacity to tolerate severe water deficits. These plants generally cannot survive water potentials below –4 MPa and their vegetative tissues often fail when water content drops below 30-60 per cent. Interestingly, while vegetative tissues remain highly sensitive to dehydration, their seeds can typically withstand extreme desiccation, often maintaining viability at water contents as low as 8-10 per cent (Zhang and Bartels 2018).

It is widely believed that vegetative desiccation tolerance evolved from pre-existing mechanisms is originally associated with seed desiccation tolerance (Costa et al 2017). Unlike bryophytes and lichens, where vegetative desiccation tolerance is relatively common, higher plants rarely exhibit this trait in their vegetative organs.

During the evolution of early tracheophytes, ancestral desiccation-tolerance mechanisms are likely retained and selectively adapted to protect reproductive structures such as seeds, while also contributing to broader responses against abiotic stress. These evolutionary adaptations have played a critical role in ensuring plant survival and reproductive success under challenging environmental conditions.

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Acquisition of desiccation tolerance: an essential trait in orthodox seeds

Desiccation tolerance is considered an ancestral trait that likely evolved early during the transition of plants from aquatic to terrestrial habitats and it is believed that the common ancestor of all land plants possessed this capability (Oliver et al 2005). In orthodox seeds, desiccation tolerance develops during seed maturation alongside physiological dormancy, which serves to prevent vivipary or pre-harvest sprouting. This process occurs concurrently with the accumulation of metabolite reserves and ultimately leads to the formation of dry, viable seeds capable of surviving extended storage periods (Tai et al 2021).

During seed development, the accumulation of storage compounds such as seed storage proteins, oleosins and caleosins plays an essential role in enhancing desiccation tolerance. These molecules help occupy cellular space, stabilize oil bodies and improve cellular resistance to dehydration while also serving as important energy reserves during germination (Shimada et al 2018). Unlike stress-induced responses observed in vegetative tissues, desiccation tolerance in orthodox seeds is acquired through a genetically programmed developmental process rather than as a direct reaction to water deficit (Tian et al 2020).

The transition of seeds from developmental phase II to phase III is generally associated with the permanent loss of desiccation sensitivity and the establishment of full desiccation tolerance. This process is regulated by maternal abscisic acid (ABA), reserve accumulation and the synthesis of protective proteins such as small heat-shock proteins (sHSPs) and late embryogenesis abundant (LEA) proteins, which also contribute to the induction of primary dormancy (Zlotorynski 2021). These adaptations enable orthodox seeds to remain in a quiescent, dry and metabolically inactive state for prolonged periods, enhancing their capacity for dispersal and long-term survival (Yan and Chen 2020).

The extraordinary longevity of orthodox seeds highlights the effectiveness of these protective mechanisms. A notable example is the successful germination of ancient date palm (*Phoenix dactylifera*) seeds, approximately 2,000 years old, recovered from arid environments characterized by high temperatures and dry soils (Buitink and Leprince 2010). Such findings demonstrate that seeds possess highly specialized molecular systems that preserve viability even after extended periods of desiccation.

In terrestrial ecosystems, seed desiccation tolerance serves as an important adaptive strategy that promotes species persistence, facilitates dispersal and ensures survival under adverse environmental conditions or during storage (Singh et al 2015). In anhydrobiotic organisms, including desiccation-tolerant seeds, the cytoplasm enters a highly stable state in which free water is largely absent and most remaining water becomes tightly bound to macromolecules, thereby, preventing cellular damage and maintaining structural stability (Ballesteros et al 2017, Privalov and Crane-Robinson 2017).

Interestingly, orthodox seeds and resurrection plants appear to share similar protective mechanisms for coping with severe dehydration, making them valuable model systems for understanding the fundamental basis of desiccation tolerance (Costa et al 2017, Farrant et al 2015). Furthermore, desiccation tolerance can be experimentally re-induced in germinated orthodox seeds through the application of ABA, providing a useful tool for investigating the regulatory pathways involved in this process (Bewley 1979).

To survive repeated cycles of drying and rehydration, seeds undergo a complex series of structural, metabolic, chemical, mechanical and molecular adjustments. For a seed to be considered desiccation tolerant, it must be capable of minimizing cellular damage during dehydration, maintaining physiological integrity in the dry state and efficiently repairing damage upon rehydration, particularly to membranes, membrane-bound organelles and genetic material (Bailly 2019).

Several protective compounds contribute to these mechanisms. Certain oligosaccharides, particularly members of the raffinose family, protect cellular structures and DNA from hydrolytic damage through a water replacement mechanism (Tian et al 2020, Delwiche and Cooper 2015). Similarly, various classes of small heat-shock proteins accumulate during late seed maturation and disappear rapidly after germination.

In addition to contributing to the formation of the intracellular glassy matrix, these proteins assist in protein folding, intracellular transport and the prevention

of irreversible protein aggregation during dehydration stress (Kalemba and Pukacka 2007, Waters and Vierling 2020, Lee et al 1997, Omar et al 2011). Together, these coordinated protective systems ensure seed survival and successful germination under favourable environmental conditions.

The protective role of intrinsically disordered LEA proteins

Desiccation-tolerant cells may contain up to 20 per cent intrinsically disordered proteins, including late embryogenesis abundant (LEA) proteins and small heat-shock proteins (sHSPs), both of which play crucial roles in protecting cellular integrity during dehydration. LEA proteins, also known as hydrophilins, are a highly conserved group of unstructured and strongly hydrophilic proteins widely distributed throughout the plant kingdom.

Under hydrated conditions, these proteins generally remain in a largely unstructured form; however, upon drying, many LEA proteins undergo conformational changes and adopt more organized structures, often developing alfa helical configurations. Although LEA messenger RNAs can be detected 10-20 days before their accumulation, the proteins themselves predominantly appear during the seed maturation stage, suggesting that their abundance is regulated through post-transcriptional mechanisms (Saighani et al 2021, Cherussery et al 2015).

LEA proteins are primarily localized in the cytoplasm and nucleus, where they play a vital role in preserving cellular structures and maintaining hydration during periods of water deficit. Their conserved three-dimensional structure allows them to stabilize proteins and membranes, preventing denaturation and aggregation of cellular components under dehydration stress (Chakrabortee et al 2012).

Interestingly, only a limited number of LEA proteins demonstrate particularly strong anti-aggregation properties. In orthodox seeds, these proteins provide additional protection by preventing macromolecular crowding and aggregation as water is removed and the distance between cellular components decreases (Artur et al 2019).

Genomic studies have identified extensive families of LEA genes in various plant species. For example, 51 genes encoding LEA proteins have been identified in the *Arabidopsis* genome (Azarkovich 2020), while 21 LEA-related genes along with two functionally characterized genes have been reported in the resurrection plant *Xerophyta viscosa* (Farrant et al 2015). Among the different LEA protein families, dehydrins are the most extensively studied and are recognized for their important role in desiccation tolerance (Radwan et al 2014). A reduction in dehydrin levels during seed germination has been associated with increased sensitivity to desiccation, further emphasizing their protective significance (Hundertmark and Hincha 2008).

Compared to vegetative tissues, seeds generally exhibit much higher levels of LEA gene expression (Amara et al 2014). The accumulation of specific LEA proteins during seed development is considered a key factor in achieving desiccation tolerance (Dussert et al 2018, Gechev et al 2012). Although LEA proteins were initially associated with seed desiccation tolerance, they have also been shown to contribute to the desiccation resistance of vegetative tissues in resurrection plants (Gechev et al 2012). In orthodox seeds, LEA proteins are abundant in the dry state, but their concentration declines during germination as seeds gradually lose desiccation tolerance (Dussert et al 2018).

Beyond seeds, LEA proteins have also been detected in seedlings, stems, leaves and roots in response to abiotic stresses such as drought, salinity, heat and cold. The presence of LEA genes in non-plant organisms, including anhydrobiotic bacteria and invertebrates, suggests that these proteins may represent a conserved mechanism of desiccation tolerance across diverse forms of life (Wise 2003).

Structurally, LEA proteins are highly hydrated and function as molecular chaperones, helping stabilize denatured proteins and promoting their proper refolding during cellular dehydration (Dussert et al 2018). Their intrinsically disordered nature enables them to form protective hydration shells around biomolecules, thereby, preserving the three-dimensional structure of enzymes and other essential cellular constituents. This mechanism helps retain residual water and prevents irreversible damage caused by denaturation (Cuevas-Velazquez et al 2017).

LEA proteins are also thought to play an important role during the early stages of seed imbibition. Their synthesis may depend either on stored messenger

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RNA accumulated during seed maturation or on new transcription initiated at the onset of water uptake, highlighting their importance in facilitating successful reactivation of metabolism during germination (Sajeev et al 2019).

Intracellular glassy state in dry seeds: a state for survival

During seed maturation, the gradual loss of water leads to the formation of a so called cytoplasmic glass, an amorphous and highly viscous matrix that resembles a solid state in which molecular mobility and relaxation rates are greatly reduced (Buitink et al 1998). This 'glass state' is thermodynamically unstable but provides essential protection during desiccation by stabilizing cellular structures and reducing biochemical activity. The formation of this highly viscous intracellular environment is promoted by low cellular water content and is strongly associated with improved seed longevity and storage stability (Su 1997).

A key contributor to glass formation is the accumulation of soluble sugars, which create a vitrified matrix that immobilizes macromolecules and protects both proteins and membranes from structural damage (Fernandez-Marin et al 2013).

Membrane stabilization is particularly critical, as cellular membranes are considered one of the primary targets of desiccation-induced injury. Severe dehydration can result in increased intracellular solute concentrations, altered molecular interactions, coalescence of oil bodies, disruption of membrane integrity and protein misfolding, all of which threaten seed viability (Shimada et al 2018).

Lipid bodies within seeds serve as important storage sites for energy reserves and protect lipids from oxidation and hydrolysis until germination and seedling establishment. These lipid reserves are stabilized by structural proteins such as oleosins and caleosins, which act as natural emulsifiers and maintain the integrity of oil bodies during drying and storage. In addition to these proteins, certain non-reducing oligosaccharides play a vital role during anhydrobiosis by effectively replacing water molecules around cellular structures, thereby, preserving their functionality and stability under dehydrated conditions (Li et al 2017).

As dehydration progresses, the substitution of water by protective sugars becomes increasingly important. Non-reducing oligosaccharides not only replace water but also contribute to the formation and maintenance of the cytoplasmic glass. When combined with highly hydrophilic proteins such as late embryogenesis abundant (LEA) proteins, these sugars enhance both the quality and persistence of the glassy state, thereby, improving desiccation tolerance (Buitink and Leprince 2008). Fully hydrated cells generally contain lower concentrations of these sugars, whereas, dehydrated cells accumulate significantly higher amounts to support cellular protection.

In desiccation-tolerant pteridophytes and angiosperms, additional protective mechanisms accompany sugar accumulation. These include increased vacuolation and activation of cell wall folding, which help cells tolerate the mechanical stresses caused by substantial water loss (Oliver et al 2020). Soluble sugars also help stabilize vacuoles, replace water molecules in membranes and macromolecules and contribute to the formation of vitrified cytoplasm (Verhoeven et al 2018).

Vitrification can, therefore, be understood as the transformation of hydrophilic cytoplasmic components into a stable glass-like state during the desiccation process (Sakurai et al 2008).

The ability of sugars to vitrify is a common and essential characteristic in desiccation tolerance. This biological glass behaves as a highly viscous liquid that immobilizes macromolecules, thereby preventing denaturation, structural disruption and most enzymatic reactions that could otherwise damage cellular components during dehydration (Golovina et al 1997, Ballesteros and Walters 2011). The stability provided by this glassy matrix helps preserve both the structural and functional integrity of important biomolecules, including enzymes. As a result, the secondary structures of proteins in dried viable seeds can remain remarkably stable and largely unchanged even after decades of storage (Zhang et al 2021).

The concept that drying seed cytoplasm enters a protective glass state has been explored and debated since the 1980s and is now widely recognized as a fundamental mechanism underlying seed longevity and desiccation tolerance (Carniel et al 2020). Several sugars have been identified as important contributors to this process, including sucrose, which serves as the primary protective sugar, as well as trehalose and raffinose-family oligosaccharides such as raffinose, stachyose and verbascose. Less common sugars,

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including octulose, may also play important protective roles (Cherussery et al 2015, Leprince and Buitink 2015).

As seeds mature, they accumulate not only non-reducing carbohydrates but also LEA proteins, both of which act synergistically to enhance cellular stability during desiccation. Studies in wheat have demonstrated a close relationship between sugar accumulation and LEA protein expression (Boudet et al 2006).

Proteomic analyses have further identified specific subsets of LEA proteins associated with survival in the dry state, suggesting that these proteins may play a direct role in stabilizing and maintaining the integrity of the intracellular glass matrix (Cuevas-Velazquez et al 2016). Together, these coordinated biochemicals and structural adaptations form the basis of effective desiccation tolerance and long-term seed viability.

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ABI3 is a master regulator of desiccation tolerance in seeds

The acquisition of desiccation tolerance is governed by a series of complex molecular and physiological processes that enable seeds to survive extreme dehydration. These processes include the accumulation of protective compounds such as soluble carbohydrates, antioxidants and late embryogenesis abundant (LEA) proteins, along with the suppression of energy metabolism and photosynthetic activity (VanBuren 2017). Together, these adjustments reduce cellular damage and prepare the seed for entry into a metabolically quiescent state. The regulation of these events is tightly controlled by plant hormones, particularly abscisic acid and by specific transcription factors such as ABI3 and ABI5, which coordinate the expression of genes involved in desiccation tolerance and seed maturation (Tian et al 2020).

The evolutionary significance of ABA in desiccation tolerance is highlighted by the presence of ABA biosynthesis and signaling genes even in basal land plants such as bryophytes. These genes are believed to have played a fundamental role in the early development of desiccation tolerance mechanisms during plant evolution (Delmas et al 2013). Tang et al (2025) highlighted the critical effects of temporal signals on seed germination and clarified the mechanism through which the EC components antagonize ABI3 and ABI5 to facilitate the crosstalk between the clock and ABA signaling pathways.

Among these transcription factors, ABI3 plays a central role by specifically activating a wide range of developmental and metabolic genes required during seed maturation. The close relationship between ABA signaling and LEA protein accumulation is evident from the fact that more than 82 per cent of LEA gene promoters in *Arabidopsis* contain the ABA-responsive element (ABRE) motif, indicating that their expression is strongly regulated through ABA-dependent pathways. In seeds at the onset of germination, ABI3 expression is typically suppressed, reflecting the transition from a desiccation-tolerant to a metabolically active state. Notably, ABI3 has been found to exhibit the strongest association with genes involved in desiccation tolerance (Sano et al 2016).

The expression patterns of ABI3 and ABI5 may vary depending on species and developmental stage. For example, contrasting expression patterns of these transcription factors have been observed during the development of *Castanospermum australe* seeds compared to *Medicago truncatula*. While ABI5 appears to negatively influence seed germination, it does not significantly affect the establishment or degree of seed dormancy (Sano et al 2016). Despite such variations, ABA-mediated signaling through the ABI3 pathway remains highly conserved across plant species and is considered essential for the acquisition of desiccation tolerance (Oliver et al 2005).

In addition to biochemical and transcriptional changes, seed desiccation also induces important structural modifications at the cellular level. During the drying process, chromatin undergoes significant yet reversible condensation, accompanied by a marked reduction in nuclear size (Van Zanten et al 2012). This chromatin condensation is thought to be a carefully regulated developmental event rather than a direct consequence of dehydration itself. Evidence suggests that ABI3 may play an important role in controlling this nuclear reorganization, further emphasizing its central function in coordinating multiple aspects of seed desiccation tolerance (Roscoe et al 2015). Together, these hormonal, genetic and structural mechanisms form an integrated regulatory network that ensures successful seed maturation, desiccation tolerance and long-term survival under adverse environmental conditions.

CONCLUSION

Desiccation tolerance is a highly specialized and evolutionarily conserved trait that enables seeds to withstand severe dehydration while preserving viability and germination potential. Its successful acquisition during seed maturation depends on a complex interplay of physiological, biochemical and molecular processes, including dormancy induction, accumulation of protective metabolites, intracellular vitrification and activation of regulatory pathways mediated by ABA and key transcription factors such as ABI3.

Protective molecules, particularly LEA proteins and soluble sugars, play indispensable roles in stabilizing cellular structures and maintaining functional integrity during drying and subsequent rehydration.

The remarkable longevity of orthodox seeds demonstrates the effectiveness of these adaptive mechanisms and highlights their importance in natural ecosystems as well as seed conservation programmes.

Advancing our understanding of desiccation tolerance not only provides valuable insights into plant evolutionary biology but also offers promising opportunities for improving seed storage technologies, safeguarding genetic resources and developing stress-resilient crops in the face of global climate change.

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