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Review / Revue

Seed longevity: Survival and maintenance of high germination ability of dry seeds

Loïc Rajjou [a,b,*], Isabelle Debeaujon [a]

[a] *UMR204, Institut national de la recherche agronomique-AgroParisTech "laboratoire de biologie des semences", Institut Jean-Pierre-Bourgin-Institut national de la recherche agronomique, route de St-Cyr, 78026 Versailles cedex, France*
[b] *UMR 204, Institut national de la recherche agronomique-AgroParisTech "laboratoire de biologie des semences" AgroParisTech, 16, rue Claude-Bernard, 75231 Paris cedex 05, France*

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Abstract

The seed constitutes the main vector of plant propagation and it is a critical development stage with many specificities. Seed longevity is a major challenge for the conservation of plant biodiversity and for crop success. Seeds possess a wide range of systems (protection, detoxification, repair) allowing them to survive in the dry state and to preserve a high germination ability. Therefore, the seed system provides an appropriate model to study longevity and aging. ***To cite this article: L. Rajjou, I. Debeaujon, C. R. Biologies 331 (2008).***
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Résumé

Longévité des graines : Survie et maintien d'un haut potentiel germinatif des graines sèches. La graine constitue le principal vecteur de multiplication chez les végétaux et c'est un stade de développement critique qui présente de nombreuses spécificités. La longévité des graines est une problématique centrale aussi bien pour la conservation de la biodiversité que pour le succès des cultures végétales. La graine possède une grande diversité de systèmes (protection, détoxication, réparation) lui permettant de se conserver à l'état sec et de maintenir sa capacité germinative. La graine est ainsi un modèle approprié pour étudier la longévité et le vieillissement. ***Pour citer cet article : L. Rajjou, I. Debeaujon, C. R. Biologies 331 (2008).***
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Keywords: Seed; Germination; Longevity; Aging

Mots-clés : Graine ; Germination ; Longévité ; Vieillissement

Abbreviations: AdoMet, *S*-adenosylmethionine; APX, ascorbate peroxidase; CAT, catalase; CDT, controlled deterioration treatment; DHAR, dehydroascorbate reductase; GABA, γ-aminobutyric acid; GSHPx, glutathione peroxidase; GSSGR, glutathione reductase; HSF, heat stress transcription factor; HSP, heat shock proteins; LEA, late embryogenesis abundant; MDHAR, monodehydroascorbate reductase; PA, proanthocyanidin; PARP, poly(ADP-ribose) polymerases; PIMT, protein L-isoaspartyl *O*-methyltransferase; POD, peroxidases; PPO, polyphenol oxidases; ROS, reactive oxygen species; SBP, seed biotinylated protein; SOD, superoxide dismutase; SSADH, succinic-semialdehyde dehydrogenase; TT, transparent testa.

* Corresponding author at: UMR204, Institut national de la recherche agronomique-AgroParisTech "laboratoire de biologie des semences", Institut Jean-Pierre-Bourgin-Institut national de la recherche agronomique, route de St-Cyr, 78026 Versailles cedex, France.
E-mail address: loic.rajjou@agroparistech.fr (L. Rajjou).
URLs: http://www.seed-proteome.com, http://www.ijpb.versailles.fr/.

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1. Introduction

Seeds of many plant species are extremely tolerant to harsh environmental conditions provided they are in a state of desiccation. In this dry state, their metabolic activity is drastically reduced to a very low level (quiescence) while retaining their ability to germinate for considerable periods (see [1] in this issue). Knowing and understanding the complex features that govern seed longevity are therefore of major ecological, agronomical and economical importance. Indeed, seeds constitute the main system for plant propagation. In the context of climate change, plant genetic composition may change in response to the selection pressure and some plant communities or species associations may be lost as species move and adapt at different rates (for an example on such ecological aspects, see [2,3]). Seed conservation (in situ or ex situ) is one of the best strategies for the conservation of plant diversity. Spectacular cases of seed longevity have been reported. Thus, radiocarbon dating allowed the determination of the age of date (*Phoenix dactylifera* L.) seeds at about 2000 years [4], sacred lotus (*Nelumbo nucifera*) seeds at 1300 years [5] or canna (*Canna compacta*) seeds at 600 years [6]. Almost 130 years ago, Michigan botanist William Beal addressed this question by stirring ordinary plant seeds into damp sand and sorted the sand into 20 clear glass bottles. Then the bottles were buried uncorked in soil at Michigan Agricultural College and periodically excavated for scoring seed viability. After more than a century, the world's longest seed viability experiment keeps inspiring scientists worldwide [7]. Although this exceptional longevity is well documented, much less is known on the mechanisms underlying this trait. To this end, a growing number of scientists are now exploring the mystery of seed longevity by molecular genetics. Why do some plant seeds hang on for decades, even centuries, while others barely survive winter? And how? These questions are complex and difficult to address experimentally. For example, it is noted that seeds exhibiting such exceptional longevity have been collected in soil (e.g., beneath rubble in [4]). Yet, paradoxically, a number of laboratory studies conducted with desiccation-tolerant (orthodox) seeds tend to show that low relative humidity and low temperature or cryopreservation might correspond to the optimal storage conditions to improve seed life span [8], lending credibility to the concept of the Svalbard Global Seed Vault as a means to provide the best possible assurance of safety for the world's crop diversity (http://www.croptrust.org/main/arctic.php?).

A recent investigation reported a large heterogeneity and inequality for longevity between seeds originating from different plant species [9]. When seeds deteriorate during storage, they lose vigor, become more sensitive to stresses during germination and ultimately become unable to germinate (Fig. 1). The rate of aging is strongly influenced by environmental and genetic factors such as storage temperature, seed moisture content, and seed quality [9,10]. Genetic approaches in rice (*Oryza sativa*) [11] and Arabidopsis (*Arabidopsis thaliana*) [12,13] showed that seed longevity is controlled by several genetic factors, allowing the detection of quantitative trait loci (QTL). Global approaches such as transcriptome and proteome profiling [14] also proved useful for the characterization of potential biomarkers of seed vigor. However, our knowledge of the exact mechanisms underlying extreme longevity of dry seeds is still in its infancy.

To study the mechanisms of seed vigor loss during storage, a seed treatment known as controlled deterioration treatment (CDT) is widely used [15]. This treatment is presumed to mimic natural aging [16], while allowing to considerably accelerate experimentally the aging rate (days compared to years), which is convenient for quickly assessing the vigor potential of seeds. Therefore, seed companies largely rely on this treatment as a prognosis for seed vigor and longevity. Furthermore, the recent progress in molecular genetics, proteomics and physiology from the use of the crucifer model plant Arabidopsis [17] now allows starting dissecting the complex mechanisms of seed aging. Several arguments demonstrate that nature has evolved complex systems of protection, detoxification and repair, in order to optimize seed life span.

2. Protection

2.1. Role of the testa: structure and composition

The seed coat or testa is a maternal tissue of ovular origin surrounding the embryo and the nutritive tissues (Fig. 2A). It consists of the integument(s) and the chalazal region, which differentiate into several layers of specialized cell types upon fertilization before dying and dramatically compressing in the mature seed coat [18,19] (Fig. 2B). In Arabidopsis, the integumentary cell layers have different fates. The innermost layer or endothelium (ii1 layer) accumulates proanthocyanidins (PAs) also called condensed tannins. These polymeric flavonoids accumulate in vacuoles as colorless compounds during early seed development and become oxidized into brown pigments by the laccase-type polyphe-

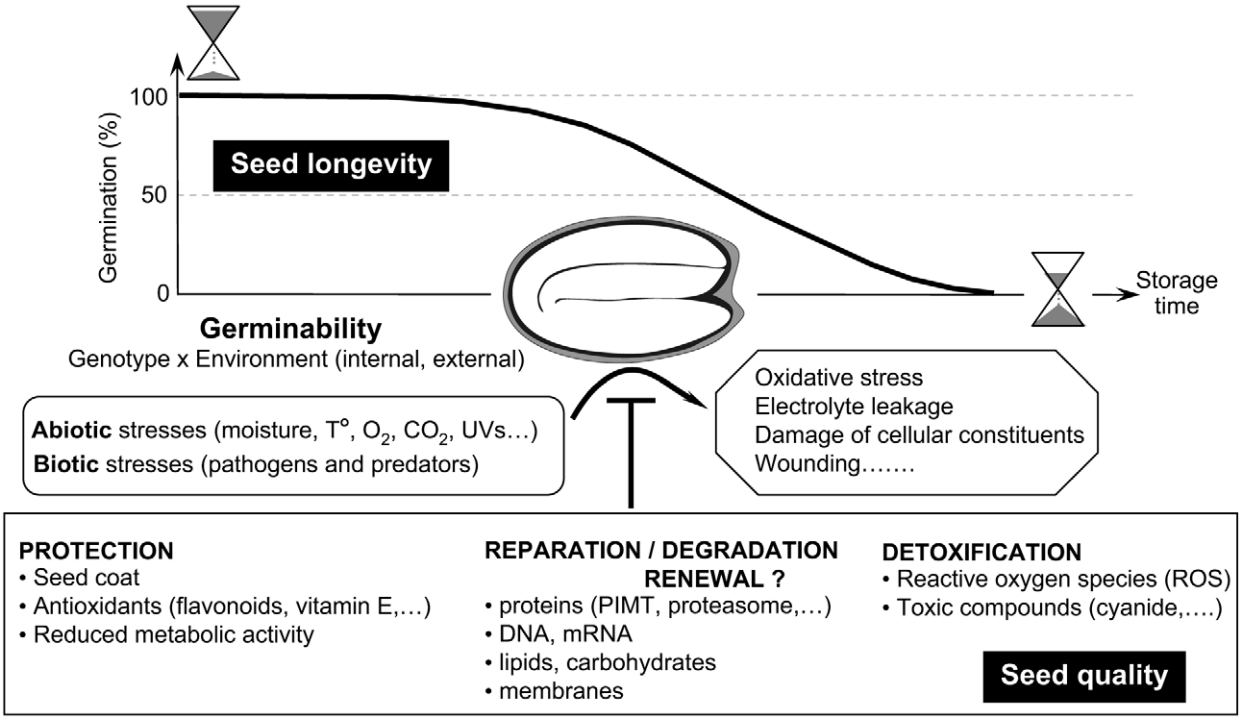

Fig. 1. Schematic presentation of the main interactive parameters determining seed longevity. Seed deterioration during storage in soil or in genebanks is generally appreciated as germinability in function of storage time. It results from the interaction between endogenous parameters defining seed quality and environmental parameters such as biotic and abiotic stresses prevailing during storage. The arrow indicates induction and the blunt end stands for repression.

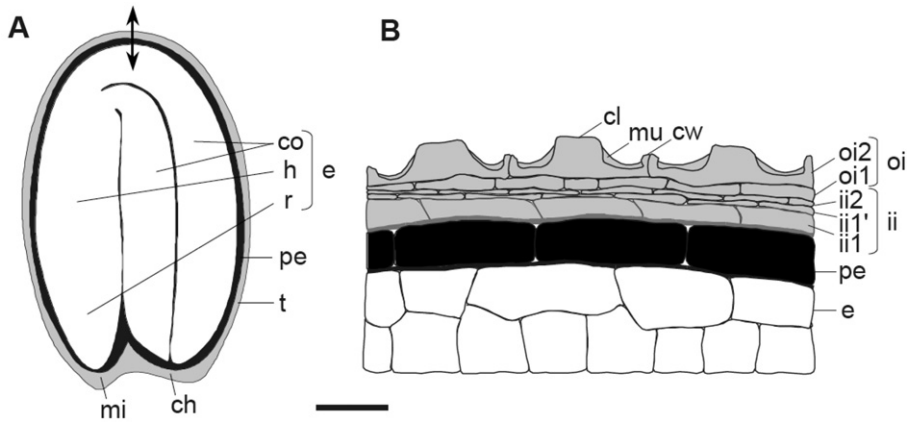

Fig. 2. Schematic organization of a mature Arabidopsis seed. (A) Seed longitudinal section. In Arabidopsis, the embryo is enclosed in one-cell-layered endosperm (peripheral endosperm or aleurone layer) tightly associated with the testa. (B) Magnification of a seed coat transversal section (at the level of the double arrow in A). Five cell layers form the two integuments. The ii1 and oi1 layers accumulate flavonoids (proanthocyanidins and flavonols, respectively) and the oi2 layer contains mucilage. ch, Chalaza; cl, columella; co, cotyledon; cw, cell wall; e, embryo; h, hypocotyl; ii, inner integument; mi, micropyle; mu, mucilage; oi, outer integument; pe, peripheral endosperm (aleurone layer); r, radicle; t, testa. Bar = 100 μm in (A) and 10 μm in (B). Adapted from Debeaujon et al. [19].

nol oxidase TRANSPARENT TESTA (TT) 10 during seed desiccation [20,21]. The subepidermal cell layer (oi1) undergoes secondary thickening of the inner tangential cell wall and accumulates colorless to pale yellow flavonoids called flavonols [21]. Many functions involved in flavonoid metabolism have been identified by a mutant approach based on visual screening for changes in seed color, from pale brown to yellow (for

a review, see [22]). The epidermal layer (oi2) differentiates into cells with thickened radial walls and central elevations known as columella producing mucilage. This one is composed primarily of the hydrophilic pectin domain rhamnogalacturonan I, which bursts out of the epidermal cells on imbibition to surround the seed [23]. The chalazal region also undertakes PA biosynthesis in a few specific cells (pigment strand) and hydrophobic suberin deposition at the hilum [19,24].

The seed coat performs important functions to protect the embryo and seed reserves from biotic and abiotic stresses during storage (pathogen and predator attacks, UV radiations, moisture, elevated temperature, oxygen, etc...). The germination of Arabidopsis mutant seeds exhibiting testa defects, such as *transparent testa (tt)* mutants (showing a modified testa flavonoid composition [22]) and *aberrant testa shape (ats)* mutant (which lacks two of the testa cell layers among five) is reduced compared to wild type (WT) following either long-term ambient storage or controlled deterioration [13,18]. Yellow-seeded rapeseed (*Brassica napus*) (see [25] in this issue) and flax (*Linum usitatissimum*) mutants exhibited higher tendency of germination loss compared to dark seeds after accelerated aging [26,27]. The antioxidant flavonoids may scavenge radical oxygen species (ROS) and therefore contribute limiting oxidative stress [28]. Testa flavonoids such as PAs provide a chemical barrier against infections by fungi due to their antimicrobial properties [29]. They also increase impermeability to solutes [18,30] and limit imbibitional damage due to solute leakage by decreasing testa permeability to water, particularly in legume seeds (for a review, see [19]). PAs were shown to deter, poison or starve bruchid larvae feeding on cowpea (*Vigna unguiculata*) seeds during storage [31]. Defense-related proteins such as polyphenol oxidases or PPOs (catechol oxidases and laccases), peroxidases (PODs) and chitinases, are prevalent in testa of Arabidopsis and soybean (*Glycine max*) [20,21,32]. The Arabidopsis TT10 laccase is present in young colorless seed coats. During the desiccation phase, the oxidation of soluble PAs into quinonic compounds by TT10 might increase their capacity to bind to the cell wall, where they would settle preventively a physico-chemical protection against potential stresses. A positive correlation exists between PA oxidation and their cross-linking to the cell wall. During desiccation of pea (*Pisum sativum* L.), cotton (*Gossypium hirsutum*) or prickly fanpetals (*Sida spinosa* L.) seeds, flavonoids accumulated in seed coats are oxidized in the presence of PPOs or PODs, leading to seed coat browning and impermeability to water. The formation of antimicrobial quinones and insoluble polymers would explain the reinforcement of the seed coat barrier to water and oxygen permeation, mechanical damage and biotic and abiotic stresses [20]. The lignin content in soybean testa also correlates with seed permeability and resistance to mechanical damage [19]. In Arabidopsis, chalazal suberin deposition also increases hardseededness [24]. Aged seeds are less tolerant than fresh seeds to aluminum toxicity upon germination, due to increased testa permeability caused by physical damage during storage time [33]. The ability of seeds to form a mucilage layer when wetted by night dew helps maintain seed viability under detrimental desert environment by enabling DNA repair [34].

A better understanding of the genetic and molecular events taking place during testa development and differentiation will not only improve fundamental knowledge on the important contribution of this multifunctional organ in seed biology, but also may open the way toward: (1) the discovery of molecular markers linked to precise testa quality parameters improving longevity, which can be used in plant breeding; and (2) the genetic engineering of these testa characters to fulfill requirements for seed longevity. Fundamental knowledge obtained in Arabidopsis testa will speed up the improvement of seed longevity in crop plants.

2.2. *Protective chemical compounds: flavonoids, vitamin E and GABA*

Accumulation of antioxidant components in dry seeds during the late maturation step on the mother plant contributes to control their storability potential. The protective role of antioxidant secondary metabolites such as flavonoids and vitamin E (tocopherols and tocotrienols) during aging or oxidative stress is well documented.

The previous paragraph exemplified the important role played by flavonoids in seed protection during storage when present in the seed coat. In Arabidopsis, flavonols are abundant also in the embryo where they can exert their protective action by scavenging ROS and protecting membranes by limiting lipid peroxidation [28]. It is very likely that flavonoid protective role at the cell level is not due exclusively to their antioxidant and prooxidant properties. Indeed there is increasing evidence that flavonoids may also have signaling functions [28].

Tocopherols (vitamin E) are lipophilic antioxidants that are very abundant in seeds. It was conclusively demonstrated using Arabidopsis mutants affected in vitamin E biosynthesis (*vte1* and *vte2* mutants) that the primary function of tocopherols in plants is to limit

nonenzymatic lipid oxidation during seed storage, germination and early seedling development [35]. The authors stress the need to determine the precise mechanism(s) causing seed longevity loss during natural and accelerated aging treatments in tocopherol-deprived *vte* mutants. Besides tocopherols, tocotrienols, which differ structurally from tocopherols by the presence of three trans-double bonds in the hydrocarbon tail, are widely found in leaves [36] and also in seeds [37]. These molecules have been shown to function in vivo as efficient antioxidants protecting membrane lipids from peroxidation [36]. In seeds their presumed function is to protect storage oil from oxidative damage [37]. In agreement with this, tocotrienols were found to be uniquely restricted to endosperm tissue of grape seeds [37].

We have identified the presence of the mitochondrial succinic-semialdehyde dehydrogenase (SSADH) in the Arabidopsis proteome from dry mature and germinating seeds (Rajjou et al., unpublished data; http://www.seed-proteome.com). SSADH is one of the three enzymes involved in the γ-aminobutyric acid (GABA) shunt. In plants, the role of the GABA shunt in protection against oxidative stress has been demonstrated [38]. The presence of SSADH in dry seeds suggests that the GABA shunt is involved in the control of seed longevity or/and germination.

Scavenging of ROS is also known to be undertaken by glutathione, ascorbic acid (vitamin C) and peroxiredoxins. However, if the metabolism of these systems presents major changes during seed desiccation and dry storage (for a review, see [39]), their role in protection against seed aging in the dry state remains to be ascertained.

2.3. Protective proteins

Quite surprisingly, several investigations clearly show that, despite a metabolically quiescent state and a low water content of desiccation-tolerant seeds, molecular and metabolic changes can occur during dry storage of mature seeds. Seed longevity markedly decreases upon water content increase. The very low water content found in mature dry seeds (orthodox seeds) is associated with a very high cytoplasmic viscosity and a very low cellular mobility due to the onset of the glassy state (see [29]). These properties allow maximum metabolism reduction in order to curtail the production of toxic compounds (e.g., ROS, cyanide, etc...) and to prevent membrane, DNA and protein damages. A very strong correlation has been demonstrated between the intercellular molecular mobility and seed life span [1, 40].

In orthodox seeds, desiccation tolerance and maintenance of a quiescent state are associated with the presence of particular proteins such as the late embryogenesis abundant (LEA) proteins, heat shock proteins (HSPs) and seed storage proteins. A close relationship seems to exist between the abundance of certain of these proteins and seed longevity. To illustrate this issue, it has been shown that a viviparous pea mutant embryo, which is intolerant to dry storage, is unable to accumulate the seed biotinylated protein, SBP65. The function of this protein, which belongs to the group 3 of LEA proteins, is thought to store biotin during maturation and to release free biotin during germination to allow resumption of metabolic activity since this molecule is the co-factor of house-keeping metabolic enzymes [41]. However, a structural function of SBP65 in the protection of cellular structure during seed desiccation and storage could not be excluded [42]. The importance of HSPs abundance in mature seeds has recently been revealed in the context of seed longevity, as transgenic Arabidopsis seeds over-accumulating a heat stress transcription factor (HSF) exhibit enhanced accumulation of HSPs and improved tolerance to aging [43]. HSPs are molecular chaperones playing an important role in protein folding and stability and also in protein protection against oxidative damage [44]. Interestingly, 12S storage protein subunits (the major seed storage proteins in dicot seeds, see [45] in this issue) have been described as being extremely sensitive to oxidative stress [44,46, 47]. The high specificity of oxidation of these major seed proteins raises the hypothesis that they can act as a trap for reactive oxygen species (ROS) to protect cellular structures and other seed proteins against oxidative stress. In this context, it is noted that several Arabidopsis seed mutants (e.g., *abi*3, *lec*1) with lower seed storage protein content than wild type display reduced seed longevity.

3. Detoxification

3.1. Reactive oxygen species

Each stage of seed life is associated with developmentally regulated changes in ROS content that may be either beneficial or deleterious (see [48] in this issue). It has become increasingly accepted that damage resulting from ROS or oxidative stress plays a role in the seed aging process. As mentioned above, dry seeds are well equipped to confront oxidative stress through a large diversity of antioxidant compounds. Besides

their metabolically quiescent state, dry seeds can endure auto-oxidation reactions leading to a progressive accumulation of ROS during storage. Oxidative stress can occur due to an imbalance in prooxidant and antioxidant levels. ROS are highly reactive and may modify and inactivate proteins, lipids, DNA, and RNA and induce cellular dysfunctions [49]. Proteins are major targets for oxidants as a result of their abundance in biological systems (particularly in seeds), and their high rate constants for reaction [50]. Previous studies indicated the presence of a large number of proteins involved in oxidative stress response in dry mature seeds and in germinating seeds. For example, it is worth noting that several studies have documented that the production of ROS during after-ripening, aging and germination entails various but specific seed protein damages [39,44,46,51,52]. However, oxidative metabolism in seeds is not necessarily a deleterious process as it seems closely associated with completion of the germination process [48]. In order to control free radical-induced cellular damage, seeds have developed a detoxification mechanism. This detoxification system includes a number of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione peroxidase (GSHPx), and glutathione reductase (GSSGR) [39,48]. Recent data indicated that a large number of these enzymes involved in ROS detoxification are present in dry mature seeds and in germinating seeds [52]. It is also worth noting that many of the oxidized (carbonylated) proteins found in Arabidopsis dry mature seeds and germinating seeds [44] have previously been identified as thioredoxin targets in wheat (*Triticum aestivum*) seeds [53]. The results lend further support for the existence of a link between ROS and redox regulatory events catalyzed by thioredoxin in seeds [54]. The detoxification potential of seeds might be strongly altered if these enzymes were to undergo some damage during seed storage, leading to a reduction of seed vigor. Under conditions where such damages do not reach a critical level, the detoxification potential of the seed can be restored by a priming treatment, an invigoration treatment of seeds based upon their controlled imbibition and ultimately improving their vigor [55]. On the other hand, when these damages accumulate to harmful levels, seeds lose their ability to control ROS and cannot endure the restart of metabolism that occurs during seed germination. This behavior is in agreement with a previous report showing that salicylic acid (an elicitor of plant defence [56]) treatment leads an improvement of Arabidopsis seed vigor in relation with an increased antioxidant capacity [47].

3.2. Removal of toxic compounds (cyanide)

ROS are not the only toxic compounds accumulating during dry seed storage and germination. However, the fate of the other toxic compounds is very poorly documented in seeds. A recent proteomic investigation highlighted that the abundance in Arabidopsis dry seeds of the β-mercaptopyruvate sulfurtransferase enzyme (MST) is correlated with seed aging [57]. Indeed, this protein is abundant in freshly harvested seeds of high vigor (i.e., characterized by a maximum germination percentage, G_{max}, of 100%). However, in 7-year-old seeds ($G_{max} = 45\%$), the accumulation level of this protein showed an important decline. MST catalyzes the transfer of sulfur from mercaptopyruvate to sulfur acceptors such as thiols or cyanide, presumably contributing to cyanide detoxification [58,59]. In plants, cyanide can be produced by various ways such as hydrolysis of cyanogenic compounds (e.g., cyanogenic glycosides and cyanolipids), decomposition of glucosinolates [60], and it can also be released as a by-product of ethylene (a gaseous plant hormone [61]) biosynthesis [62]. Although the exact origin of cyanide accumulation in seed during dry storage and germination remains unknown, the control of cyanide content seems to play an important role in seed physiology. Thus, despite the fact that low concentrations of cyanide are beneficial for releasing seed dormancy and improving germination [63], its production is often associated with deleterious mechanisms and must therefore be controlled. For example, cyanide can inhibit the activity of heme proteins as peroxidases [64,65] and catalases [66]. Moreover, this molecule is a potent inhibitor of mitochondrial ascorbate (vitamin C) synthesis in plants [67]. Thus, cyanide accumulation during seed aging could reduce the efficiency of plant cells to scavenge ROS generated during seed storage. Our results revealed for the first time that a loss in seed vigor is associated with a decreased level of MST, indicating that seeds must maintain a high ability to detoxify cyanide to protect cellular structures [57].

4. Cell repair and turnover

4.1. DNA

Accumulation of macromolecular damage, including DNA damage and genomic instability, is considered as a driving force for the aging process [68]. It is worth noting that in the framework of seed germination, cell

division is not necessary for radicle emergence [69], although a recent transcriptomic analysis showed that the activation of the cell cycle in the Arabidopsis root meristem precedes the penetration of the seed envelopes by the radicle and that D cyclins are limiting factors for this process [70]. Seeds are subject to DNA lesions, not only during desiccation but also during seed storage. Induction of DNA damage during seed aging has been demonstrated for a long time [71]. Repair mechanisms can improve subsequent performance under suboptimal conditions for germination. For this reason, their induction during invigoration treatments of seeds is of major interest for the seed industry. Such treatments, which are based upon controlled hydration of the seeds, are referred to as "priming". During treatment, seeds remain tolerant to desiccation because of incomplete hydration and can be re-dried [72]. It has been shown that DNA repair occurs during seed priming [34,73,74]. However, proteins involved in seed DNA repair mechanisms remain poorly described. DNA present in seeds encounters a very different chemical environment from that met by DNA in the nucleus of actively metabolizing cells. Not surprisingly, the activity of poly(ADP-ribose) polymerases (enzymes involved in DNA base-excision repair, DNA-damage signaling and regulation of genomic stability) was shown to be essential to initiate early germination [75]. Yet, other DNA repair mechanisms, likely involved in seed vigor, remain to be discovered. In this context, it is interesting that double mutants of the two *Zea mays* L. (maize) rad51 homlogs (proteins that plays a central role in homologous recombination and the repair of double-strand breaks) are viable and develop well under normal conditions, but have substantially reduced seed set [76]. The maintenance of a functional DNA repair complex appears therefore an essential condition for long-term survival in the dry state.

4.2. Protein synthesis and repair

It has been shown that seed germination has an unconditional necessity for protein synthesis. Thus, cycloheximide, an inhibitor of protein translation, induces a complete inhibition of Arabidopsis seed germination [30]. An interesting feature supports these observations and concerns the apparent correlation between protein translational ability and the reduction of seed vigor induced by the CDT [46,57]. This result disclosed that translational capacity can be an excellent feature for the estimation of seed ability to germinate, a finding that is in good agreement with previous work demonstrating a loss in translational capacity during seed aging in soybean [77]. *De novo* protein synthesis from stored mRNA can allow the renewal of non-functional proteins altered during storage and that are essential to initiate metabolism restart during germination [57]. An examination of published data discloses that the germination process induces an increased synthesis of several enzymes involved in methionine metabolism, namely methionine synthase, *S*-adenosylmethionine synthetase, and *S*-adenosylhomocysteine hydrolase [78]. There are several possibilities to account for this behavior. The first is reactivating cellular activity in germinating seeds owing to the general importance of methionine and *S*-adenosylmethionine (AdoMet) in plant metabolism [79]. This finding is in agreement with previous work demonstrating a requirement for Met biosynthesis in Arabidopsis seedling establishment [80]. A second possibility could be that germinating seeds have a special requirement for methionine and/or AdoMet. In this context, it is worth noting that seeds contain a very active protein L-isoaspartyl *O*-methyltransferase (PIMT), an AdoMet-dependent enzyme playing a role in limiting and repairing age-damaged aspartyl and asparaginyl residues in proteins. Indeed, naturally aged barley seeds exhibit decreased levels of PIMT activity [81], whereas seeds of sacred lotus, one of the holder of the world's record for long-term seed viability (1300 years) display high amounts of this enzyme during germination [5]. In plants, the greatest PIMT activity has been found to be localized primarily in seeds, where nonenzymatic protein damages is hypothesized to occur during dehydration and dry storage [81,82]. Such damage should be repaired for normal, vigorous germination and subsequent radicle protrusion [83–85], and would therefore necessitate a sustained production of AdoMet. Protein repair is quite cheap in term of energy requirements to restore functional activity of damaged proteins, compared to the cost of *de novo* protein synthesis. In the context of dry quiescent seeds, this strategy seems to prevail in order to initiate seed germination and metabolism restart. As mentioned above for DNA repair, the maintenance of a functional protein repair mechanism appears to be a key condition for long-term survival of seeds in the dry state

5. Concluding remarks

As fundamental knowledge on the biological basis of seed longevity is increasing, general principles of survival and maintenance of high germination ability of dry seeds are formulated that can be the starting point for future research and intervention toward achieving an endless life. This review attempted to draw attention to the evidence that a wide range of physical, chemi-

cal, molecular, and genetic factors is implicated in the control of seed longevity. The contribution of the testa to seed longevity is important for maintenance of the weakest metabolic activity and protection against various environmental stresses. Free radical-counteracting processes and detoxification mechanisms are closely related to control the prooxidant/antioxidant balance both during seed storage and germination. When the prooxidant scavenging systems are saturated, detoxification mechanisms might be affected that irreparably will lead to seed death. A better knowledge of DNA and protein protection and repair mechanisms seems promising to manipulate seed longevity. Seeds of particular plant species belong to the most spectacular examples of organism longevity in eukaryotes. Due to this property, the seed system provides an appropriate model to study longevity and aging, which is of paramount interest for human health.

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