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WHEN SEEDS BREATHE THEIR LAST: UNMASKING THE SABOTEURS OF AGEING AND PRESERVATION

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ABSTRACT

Seed ageing is an inevitable physiological process that leads to a progressive decline in seed vigor, viability, and germination capacity over time. This deterioration adversely affects crop productivity, seed trade, and the long-term conservation of plant genetic resources. The present review explores the multifaceted mechanisms underlying seed ageing and deterioration, highlighting the key physiological, biochemical, and molecular changes involved. Reactive oxygen species (ROS) accumulation, lipid peroxidation, membrane destabilization, nucleic acid degradation, and impairment of antioxidant defense systems emerge as the principal "saboteurs" that disrupt seed homeostasis. Additionally, external factors such as moisture content, temperature, and oxygen availability significantly influence the rate of deterioration. Traditional and advanced techniques used for assessing seed quality, including accelerated ageing tests, electrical conductivity, and omics-based approaches, are also discussed. Emphasis is placed on recent strategies to mitigate deterioration, such as seed priming, antioxidant application, and optimized storage conditions. The review further identifies emerging research areas and technological interventions that could enhance seed longevity. Understanding the complex interplay of internal and external factors driving seed deterioration is essential to improving storage practices and ensuring global food and seed security.

***Key words*:** Seed ageing, seed deterioration, seed vigour, reactive oxygen species (ROS), antioxidant enzymes, seed priming, storage conditions, seed longevity, molecular markers, physiological decline

Introduction

Seeds, the embryonic propagules of plants, are critical units of reproduction, biodiversity preservation, and food security. While appearing dormant, seeds remain physiologically and biochemically active and inevitably undergo ageing—a natural degenerative process marked by the gradual decline in viability, vigor, and germination potential (Bewley *et al.*, 2013; Rajjou & Debeaujon, 2008). The consequences of seed deterioration are far-reaching, affecting crop productivity, conservation programs, and seed storage efforts globally. One of the earliest and most damaging manifestations of seed ageing is the accumulation of reactive oxygen species (ROS) such as superoxide anions, hydrogen peroxide, and hydroxyl radicals. While ROS are generated as part of normal aerobic metabolism, their levels increase during storage, especially under high temperature and humidity (El-Maarouf-Bouteau & Bailly, 2008).

These highly reactive molecules initiate lipid peroxidation, protein oxidation, and nucleic acid damage, ultimately disrupting membrane integrity and metabolic homeostasis (Kranner *et al.*, 2010). Membrane degradation is widely regarded as a primary marker of seed ageing. Oxidative damage to phospholipids reduces membrane fluidity and increases permeability, leading to electrolyte leakage and energy disruption during imbibition (McDonald, 1999). These effects are exacerbated by the declining activity of antioxidant enzymes—notably superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD)—which are essential for detoxifying

ROS during early germination (Tian *et al.*, 2020). Their loss signals an imbalance between oxidative stress and defense systems in the ageing seed. Seed ageing also impacts the molecular architecture of the seed. Genetic material becomes vulnerable to oxidative damage, resulting in strand breaks and base modifications. Simultaneously, mRNA transcripts essential for early seedling development degrade or become unstable, impairing protein synthesis and metabolic reactivation during germination (Clarke & Walters, 2002). Proteomic studies have identified an accumulation of stress-related proteins and altered protein profiles in aged seeds, indicating deterioration of protein homeostasis (Gao *et al.*, 2021). Additionally, recent research points to epigenetic modifications, such as changes in DNA methylation, as potential regulators of seed viability loss (Chen *et al.*, 2022). External environmental factors significantly modulate the rate of seed deterioration. Seed moisture content, temperature, and oxygen availability are among the most influential storage parameters. Seeds stored under high humidity or elevated temperatures experience accelerated deterioration due to increased metabolic and oxidative stress (Nagel & Börner, 2016).

In contrast, long-term viability is enhanced under cool, dry, and oxygen-reduced conditions, principles applied in gene banks and seed vaults globally (Li *et al.*, 2020). Assessing the extent of seed ageing is vital for maintaining quality during storage. Traditional tools such as the standard germination test and accelerated ageing test help evaluate seed vigor and predict storability. In addition, electrical conductivity (EC) tests assess membrane integrity by measuring ion leakage from soaked seeds (Matthews *et al.*, 2012). More advanced diagnostic approaches involve tracking biochemical indicators like malondialdehyde (MDA) or using transcriptomic and proteomic markers to identify ageing-specific changes (Xin *et al.*, 2019).

To combat deterioration, several mitigation strategies have been developed. Seed priming, which involves partial hydration and controlled reactivation of metabolism, is widely recognized for improving germination performance and reducing ageing effects (Farooq *et al.*, 2019). The exogenous application of antioxidants such as ascorbate or glutathione has also shown efficacy in restoring seed vigor by neutralizing ROS (Chen *et al.*, 2021). Furthermore, innovations in packaging, such as vacuum-sealed or moisture-impermeable materials, and storage technologies like cryopreservation are increasingly employed to extend seed longevity (Hong & Ellis, 1996; Kashyap *et al.*, 2023). Beyond agriculture, seed ageing poses significant risks to genetic conservation and biodiversity preservation. In germplasm banks, where seeds of endangered, wild, or rare species are stored for long durations, even slight declines in viability can result in irreversible genetic loss (Walters *et al.*, 2005). Climate change further complicates storage protocols, as fluctuating temperatures and humidity levels challenge traditional seed preservation methods (Kundu *et al.*, 2023). Despite considerable progress, critical knowledge gaps persist. The complex interactions between oxidative damage, gene regulation, and metabolic dysfunction are not yet fully understood. Variation in ageing responses among species and even within genotypes presents additional challenges for universal preservation protocols. Integration of omics technologies—such as transcriptomics, metabolomics, and proteomics—with predictive modeling may offer more precise insights into the mechanisms underlying seed longevity (Zhou *et al.*, 2020).

This review aims to unravel the physiological, biochemical, and molecular “saboteurs” that drive seed deterioration and limit storage life. By examining both the internal damage mechanisms and external environmental influences, this article offers a comprehensive exploration of seed ageing, diagnostics, mitigation strategies, and emerging technologies. It provides an evidence-based framework to guide researchers, conservationists, and seed technologists toward innovative solutions for safeguarding seed longevity in an increasingly uncertain global climate.

Reactive Oxygen Species (ROS) – Silent Killers

Reactive oxygen species (ROS) are at the core of seed ageing and deterioration, acting as destructive metabolic by-products that silently erode seed quality over time. While low levels of ROS play signaling roles in dormancy release and early germination, their unchecked accumulation under stress or prolonged storage causes oxidative damage to critical cellular components (Bailly, 2004; Noctor & Foyer, 2016). This dual nature of ROS makes them both essential and potentially fatal for seed viability. In metabolically active seeds, ROS such as superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radicals (•OH), and singlet oxygen ($^1O_2$) are generated during mitochondrial respiration, β-oxidation of lipids, and other redox reactions (Barba-Espín *et al.*, 2012). Under optimal storage, these ROS are detoxified by antioxidant systems. However, in ageing seeds, these scavenging mechanisms decline, allowing ROS to accumulate and initiate irreversible oxidative stress (Suleiman *et al.*, 2021). One of the earliest targets of ROS in ageing seeds is the lipid bilayer of cell membranes. Polyunsaturated fatty acids (PUFAs) are particularly vulnerable to peroxidation, resulting in disintegration of membrane structure, loss of selective permeability, and increased ion leakage. Malondialdehyde (MDA), a by-product of lipid peroxidation, is a widely used biochemical marker to quantify oxidative membrane damage during seed ageing (Tao *et al*., 2022). Studies in crops like soybean, wheat, and onion confirm that elevated MDA levels correlate with reduced seed vigor and germination (Li *et al*., 2020; Basavarajappa *et al*., 2020). Proteins are another major target of ROS-induced modification. Oxidative stress can result in carbonylation, disulfide bond breakage, and enzymatic inactivation. The impairment of vital enzymes such as ATPases, dehydrogenases, and antioxidant enzymes diminishes metabolic competence, thereby contributing to delayed germination or failure of seedling establishment (Cheng *et al*., 2021).

Moreover, ROS affect protein repair systems such as methionine sulfoxide reductase, which becomes less active in aged seeds, leading to the buildup of damaged proteins (Stroher *et al*., 2016). ROS also cause extensive damage to nucleic acids. DNA strand breaks, base modifications like 8-oxoG, and impaired chromatin structure compromise transcriptional activity in aged seeds (Kurek *et al*., 2020). RNA integrity is similarly affected, with fragmentation of stored mRNA transcripts involved in germination-related proteins, rendering them non-functional during imbibition (Hu *et al*., 2021). This disrupts the synthesis of essential proteins and hampers successful germination. Interestingly, the extent of ROS accumulation and the damage it causes differ by species and genotype. For instance, studies have shown that desiccation-tolerant species possess more robust antioxidant systems that delay ageing, while sensitive genotypes deteriorate more quickly under the same conditions (Yan *et al*., 2022). In summary, ROS play a central role as biochemical saboteurs in seed ageing. Their accumulation leads to oxidative damage across membranes, proteins, and genetic material, ultimately compromising the physiological potential of seeds. A deeper understanding of ROS metabolism and their cellular targets is essential for developing strategies to mitigate deterioration and extend seed longevity.

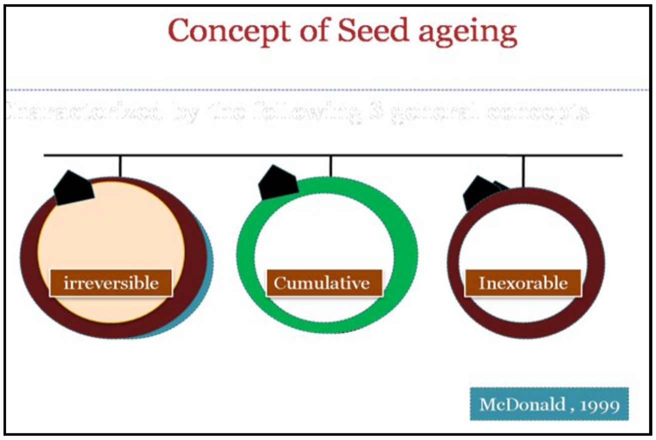

Fig. 1: Conceptual model of seed ageing showing its inexorable, irreversible and cumulative nature.

Antioxidant Defense Systems – The Frontline Soldiers

Seed ageing is fundamentally an oxidative process in which reactive oxygen species (ROS) act as destructive agents that impairs cellular integrity and function. To combat oxidative stress, seeds are equipped with a sophisticated antioxidant defense system that serves as the primary shield against ROS-induced damage. This defence mechanism comprises a coordinated network of enzymatic and non-enzymatic antioxidants that scavenge and detoxify ROS during development, storage, and germination (Apel & Hirt, 2004). The effectiveness of this system is crucial for maintaining seed viability and delaying the onset of deterioration.

Enzymatic Antioxidants: Precision Scavengers

The enzymatic antioxidant system is central to redox homeostasis in seeds. The superoxide dismutase (SOD) family serves as the first line of defense by catalyzing the dismutation of superoxide radicals (O_2^-) into molecular oxygen and hydrogen peroxide ($H_2 O_2$). Subsequently, catalase (CAT) and ascorbate peroxidase (APX) decompose H_2O_2 into water and oxygen, thereby preventing oxidative damage (Gill & Tuteja, 2010). Additionally, enzymes such as glutathione reductase (GR) and monodehydroascorbate reductase (MDHAR) function within the ascorbate–glutathione cycle, ensuring continuous regeneration of ascorbate and glutathione, two key non-enzymatic antioxidants (Foyer & Noctor, 2011). During seed ageing, the activity of these enzymes significantly declines. For example, in artificially aged sunflower and rice seeds, marked reductions in SOD and

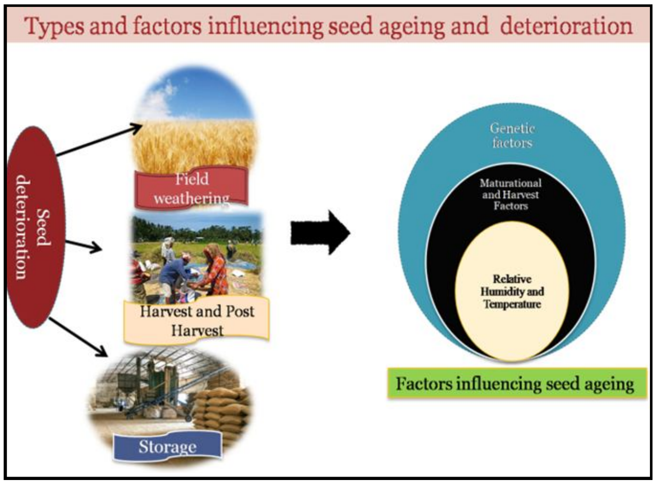

Fig. 2: Factors influencing seed ageing and deterioration illustrated by author.

Table 1: Factor affecting seed deterioration.

Factor	Effect on Seeds	Example Crops	Reference
Moisture	Promotes fungal growth, accelerates respiration & EC	Pulses, cereals	Scientific Reports, 2025
Temperature	Increases respiration, lipid peroxidation	Oilseeds	Xing *et al.*, 2025
Oxygen (ROS)	Enhances oxidative stress, damages mitochondria	Wheat, maize	Li *et al.*, 2022; Farooq *et al.*, 2021
Storage pests	Physical damage, nutrient loss	Groundnut	Trusiak *et al.*, 2022
Seed type	Recalcitrant seeds rapidly lose viability if dried	Cocoa, rubber	Review on Recalcitrant Seeds, 2023

CAT activities were reported alongside increased lipid peroxidation and electrolyte leakage (Sharma *et al.*, 2022; Verma *et al.*, 2021). These reductions compromise the seed's ability to detoxify accumulating ROS, resulting in irreversible cellular damage. Notably, primed or coated seeds often retain higher antioxidant enzyme activity, suggesting a potential avenue for extending longevity through biochemical enhancement (Singh *et al.*, 2022).

Non-Enzymatic Antioxidants: The Silent Supporters

Complementing the enzymatic machinery, non-enzymatic antioxidants such as ascorbate (vitamin C), glutathione (GSH), tocopherols (vitamin E), carotenoids, and flavonoids act as direct ROS scavengers and redox buffers. Ascorbate and glutathione, in particular, play dual roles as electron donors and substrates in regeneration cycles, contributing to ROS detoxification and cellular redox signalling (Smirnoff, 2018).

A decline in ascorbate and glutathione pools has been observed in seeds subjected to accelerated ageing, indicating oxidative stress and redox imbalance (Jiang *et al.*, 2020). Moreover, tocopherols, especially α-tocopherol, act as lipid-soluble antioxidants that prevent membrane lipid peroxidation by scavenging lipid radicals. Their protective role is well documented in long-stored seeds of Arabidopsis and maize, where higher tocopherol content correlated with delayed ageing (Wang *et al.*, 2019). Polyphenolic compounds like flavonoids also exhibit antioxidant properties by chelating transition metals and directly scavenging ROS. Recent metabolomic profiling in aged pea and soybean seeds identified significant declines in flavonoid content, suggesting their depletion during prolonged storage (Zhang *et al.*, 2021). The synergy between enzymatic and non-enzymatic antioxidants is crucial to buffering oxidative stress; disruption of either component can accelerate deterioration.

Antioxidant Imbalance: A Prelude to Ageing

The redox imbalance hypothesis posits that a shift in the cellular redox state—largely governed by the balance between ROS production and antioxidant capacity—triggers seed ageing (Bailly, 2004). In aged seeds, antioxidant capacity is not only reduced in absolute terms but also fails to adapt to increased ROS generation. This leads to a tipping point beyond which cellular homeostasis cannot be maintained. Interestingly, genotypic variability in antioxidant profiles significantly influences seed longevity. For instance, elite rice cultivars with higher baseline antioxidant enzyme activity demonstrated better storability compared to traditional genotypes (Mahmud *et al.*, 2022). Such differences underscore the importance of incorporating antioxidant potential as a trait in seed quality breeding programs.

Enhancing Antioxidant Defense: Future Opportunities

Recent research has explored methods to boost antioxidant defenses as a strategy to mitigate seed ageing. Pre-storage treatments with exogenous antioxidants like ascorbate, salicylic acid, or melatonin have shown promise in improving longevity and post-storage germination (Liu *et al.*, 2020). Genetic engineering approaches to upregulate antioxidant enzyme genes (e.g., SOD, APX) in model plants have also demonstrated improved seed vigor after storage (Wang *et al.*, 2022). Furthermore, nanotechnology-based carriers are being explored to deliver antioxidant compounds in a sustained manner during seed storage. These advancements suggest that targeted manipulation of antioxidant pathways could significantly delay the biochemical onset of deterioration.

Molecular Mechanisms of Seed Ageing: Cracks in the Genetic Core

Seed ageing is not only a physiological and biochemical process but also a molecular phenomenon involving

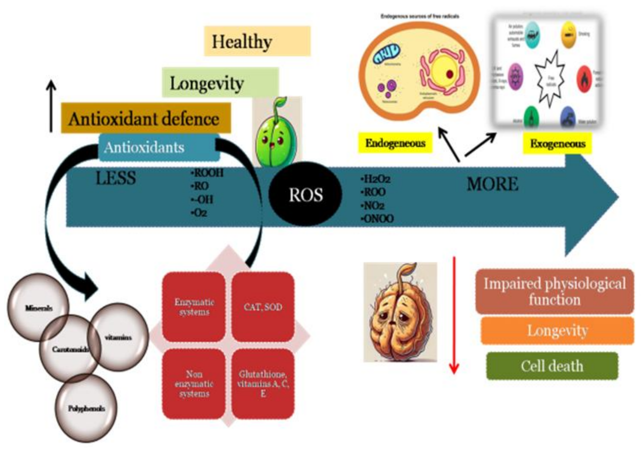

Fig. 3: Role of ROS in Seed ageing (illustrated by author).

Table 2: Biochemical changes during seed ageing.

Parameter	Change Observed	Consequence	Reference
Enzyme activity	Decline in amylase, catalase	Poor germination	Farooq *et al.*, 2021; Yue *et al.*, 2024
Membrane integrity	Loss of selective permeability	Solute leakage	Li *et al.*, 2022; Xing *et al.*, 2025
Protein degradation	Accumulation of denatured proteins	Seed vigor decline	Yue *et al.*, 2024
Lipid peroxidation	Free radical accumulation, MDA & LOX increase	Membrane damage	Yue *et al.*, 2024; Scientific Reports, 2025

irreversible damage at the genomic, transcriptomic, and proteomic levels. The cumulative molecular changes incurred during storage disrupt regulatory and developmental pathways critical for germination and seedling establishment. Understanding these alterations provides a more profound insight into how seed vigor declines with time and offers molecular targets for preservation strategies.

DNA Damage and Genomic Instability

One of the most prominent molecular consequences of seed ageing is oxidative damage to DNA, including strand breaks, base oxidation (e.g., 8-oxoguanine formation), DNA-protein cross-linking, and depurination (Waterworth *et al.*, 2010). These modifications impair replication and transcription, leading to genomic instability and loss of cellular function during early germination. Aged seeds often exhibit reduced expression of DNA repair genes, suggesting a compromised ability to rectify oxidative lesions (Macovei & Tuteja, 2012). Several studies have highlighted a decline in the activity of base excision repair (BER) and nucleotide excision repair (NER) pathways in aged seeds. For instance, research on Arabidopsis thaliana and barley has shown that genes encoding DNA glycosylases and AP-endonucleases are downregulated during ageing, increasing mutation accumulation (Cordoba Cañero *et al.*, 2014; Kocsy *et al.*, 2011). These impairments lead to disrupted chromosomal architecture, faulty cell division, and embryo lethality.

RNA Integrity and Transcriptome Degradation

Seed ageing also affects messenger RNA (mRNA), which is crucial for post-imbibition protein synthesis. Unlike DNA, mRNA lacks protective histones and repair systems, making it highly vulnerable to ROS-mediated degradation (Rajjou *et al.*, 2008). During storage, significant fragmentation and degradation of stored mRNA transcripts occur, particularly those encoding proteins related to energy metabolism, stress responses, and germination regulation (Bazin *et al.*, 2011). In soybean and wheat, transcriptomic profiling has revealed a dramatic decline in the abundance of transcripts for enzymes involved in glycolysis, the TCA cycle, and reactive oxygen species detoxification in aged seeds (Chandna *et al.*, 2020). Additionally, genes related to mitochondrial biogenesis and protein translation are often suppressed, affecting energy production and protein synthesis upon germination. RNA-binding proteins, including poly(A)-binding proteins (PABPs) and RNA helicases, are also compromised in aged seeds, impairing mRNA stability and translation regulation (Sano *et al.*, 2020). These changes reduce translational efficiency and protein turnover, which are essential for initiating growth after dormancy.

Protein Misfolding and Proteostasis Collapse

Protein integrity is another molecular aspect compromised during seed ageing. Oxidative stress leads to protein carbonylation, denaturation, and cross-linking, resulting in misfolded or non-functional proteins (Job *et al.*, 2005). Proteins such as enzymes, transcription factors, and chaperones are particularly sensitive to ROS, and their inactivation can block vital metabolic and signaling pathways. Proteomic studies in pea, sunflower, and rice seeds have reported an increased abundance of heat shock proteins (HSPs) and ubiquitin-related proteins during ageing, reflecting a stress-induced response to misfolded protein accumulation (Xin *et al.*, 2020). The ubiquitin-proteasome system (UPS), which marks and degrades oxidized proteins, becomes overwhelmed in aged seeds, leading to proteostasis collapse (Nambara & Nonogaki, 2012). This accumulation of damaged proteins contributes to metabolic dysfunction and impairs embryonic development.

Epigenetic Modifications: Silenced and Reactive Genomes

Emerging evidence suggests that epigenetic changes—including DNA methylation, histone modifications, and small RNAs—play a significant role in seed ageing and vigor regulation. DNA methylation levels, particularly at cytosine residues (5mC), tend to increase during ageing, which may lead to the repression of genes necessary for germination (Michalak *et al.*, 2021). In artificially aged *Brassica napus* seeds, differential methylation patterns were observed in genes associated with stress response, signaling, and hormone metabolism, correlating with reduced germination and viability (Liu *et al.*, 2021). Similarly, histone acetylation

Table 3: Storage methods and seed longevity.

Storage Method	Conditions	Longevity	Suitability
Traditional storage	Ambient temp & RH	1–2 years	Farmers
Cold storage	4 °C, low RH	5–10 years	Research stations
Cryopreservation	–196 °C (liquid N_2)	Several decades	Gene banks
Recalcitrant seed care	Moist, non-freezing storage	Weeks–months	Cocoa, mango, rubber

changes affect chromatin accessibility and gene expression regulation, suggesting that chromatin remodeling is involved in the response to seed ageing. Small RNAs such as microRNAs (miRNAs) have also been implicated in post-transcriptional regulation during seed deterioration. Studies in maize and rice identified differentially expressed miRNAs that regulate transcripts involved in hormone signaling, antioxidative responses, and energy metabolism under ageing conditions (Chen *et al.*, 2019). These findings suggest a multilayered epigenetic control over the seed's ability to withstand oxidative stress and initiate germination.

Integrative Omics: Systems View of Ageing

The complexity of molecular seed ageing is increasingly unraveled through multi-omics approaches, including transcriptomics, proteomics, metabolomics, and epigenomics. Integrating these datasets allows identification of critical hubs and regulatory nodes affected by ageing. For instance, combined proteomic and transcriptomic analysis in aged pea seeds revealed a coordinated decline in protein synthesis, energy metabolism, and ROS scavenging pathways (Kumar *et al.*, 2023). Such systems biology insights are pivotal for developing molecular markers of seed viability and designing interventions for enhancing longevity.

Environmental and Physiological Factors Accelerating Ageing

Seed ageing is not an isolated or uniform process; it is highly influenced by both external environmental conditions and intrinsic physiological traits. While genetic makeup and cellular defense systems determine a seed's inherent longevity, extrinsic factors like temperature, moisture, oxygen, and mechanical stress critically shape the rate and extent of deterioration. Understanding these drivers provides a framework for predicting seed shelf life and designing appropriate storage interventions.

Temperature: The Catalyst of Chemical Reactions

Temperature is one of the most influential environmental variables in seed ageing. High temperatures accelerate metabolic activity, increase lipid peroxidation, and promote ROS accumulation, hastening deterioration. The Arrhenius principle, which relates temperature to the rate of chemical reactions, underpins the sharp increase in biochemical degradation at elevated storage temperatures (Delouche & Baskin, 1973). Accelerated ageing tests often expose seeds to high temperatures (e.g., 40–45°C) to simulate ageing and assess vigor loss. Studies in maize, sunflower, and soybean have shown rapid declines in germination and membrane integrity under elevated temperatures (Demir *et al.*, 2008; Singh & Sharma, 2021). Even under ambient conditions, seeds stored in tropical climates deteriorate more quickly than those in temperate regions due to heat-induced oxidative stress.

Relative Humidity and Moisture Content: A Delicate Balance

Seed moisture content (SMC) is tightly linked to deterioration. Moisture promotes enzymatic activity, respiration, and non-enzymatic oxidative reactions, particularly in seeds stored above their critical moisture threshold (typically 8–12% depending on species). At high SMC, hydrolytic enzymes become active, degrading stored lipids, proteins, and nucleic acids (Hay *et al.*, 2013). Relative humidity (RH) of the storage environment determines seed equilibrium moisture. The Seed Viability Equation proposed by Ellis and Roberts (1980) mathematically correlates RH and temperature with seed lifespan. Seeds stored under high RH conditions experience increased aging rates, particularly in humid tropical zones. For instance, wheat seeds stored at 75% RH deteriorated significantly faster than those at 35% RH, with notable declines in vigor and enzymatic activity (Singh *et al.*, 2019).

Oxygen Availability and Oxidative Stress

Oxygen plays a dual role in seed physiology—essential for respiration but also a precursor for ROS production. Seeds stored in aerobic conditions suffer more rapid ageing due to the oxidative degradation of lipids and nucleic acids. Reduced oxygen atmospheres, including vacuum packing or nitrogen flushing, have been shown to prolong seed life by slowing oxidation (Chandel *et al.*, 2020). In barley and rice, modified atmosphere packaging (MAP) delayed the onset of lipid peroxidation and preserved germination percentage over extended storage (Kalpana *et al.*, 2021). Moreover, oxygen tension interacts with temperature and moisture, forming a triad of deterioration factors. For example, even moderately moist seeds stored in oxygen-rich and warm conditions undergo exponential degradation due to synergistic ROS generation.

Seed Composition: Biochemical Susceptibility

Physiological characteristics, especially biochemical composition, influence how seeds respond to environmental stresses. Seeds rich in polyunsaturated fatty acids (PUFAs) are more prone to lipid peroxidation. Oilseeds like soybean, sunflower, and mustard exhibit higher ageing sensitivity due to rapid rancidification of lipids (Chauhan *et al.*, 2018). In contrast, starchy seeds such as wheat and rice have better storability. The content and integrity of storage proteins also affect ageing. For example, seed storage proteins may undergo conformational changes during ageing, leading to insolubility or loss of nutritional function. Seeds with higher antioxidant content (e.g., tocopherols, flavonoids) generally exhibit greater longevity (Wettlaufer & Leopold, 1991).

Seed Maturity, Physical Integrity, and Initial Vigor

The stage at which seeds are harvested significantly influences their ageing trajectory. Immature or overmature seeds lack optimal structural and biochemical defenses and are often more susceptible to mechanical damage and fungal invasion (Basra *et al.*, 2003). Additionally, seeds with damaged seed coats allow easier oxygen and moisture infiltration, accelerating deterioration. Initial seed vigor is another determinant. High-vigor seeds possess more efficient membrane repair systems, robust antioxidant machinery, and better desiccation tolerance. Consequently, deterioration is delayed compared to low-vigor seeds even under identical storage conditions (Perry, 1980). Seed lots with mechanical injuries, cracks, or microbial contamination are particularly vulnerable.

Strategies to Delay Ageing and Enhance Seed Longevity

Seed ageing is an inevitable biological process, but its onset and severity can be significantly delayed through targeted strategies that minimize oxidative stress, preserve cellular structures, and maintain metabolic integrity. As global agriculture shifts toward long-term seed storage, conservation, and climate resilience, enhancing seed longevity has emerged as a critical focus in both commercial seed production and gene bank management. A combination of physical, chemical, physiological, and biotechnological interventions has been explored to mitigate the detrimental effects of ageing and improve storability.

Physical and Environmental Approaches

Optimizing storage conditions remains the most fundamental and effective method for preserving seed quality. As seed ageing is highly sensitive to temperature and moisture, maintaining low relative humidity (<35%) and cool to sub-zero temperatures (0°C to -20°C) is essential for slowing biochemical reactions and minimizing ROS production (Walters *et al.*, 2005). For orthodox seeds, the widely accepted "50/50 rule" suggests maintaining storage environments where the sum of temperature (°F) and relative humidity (%) does not exceed 100 (Justice & Bass, 1978). Vacuum packaging and modified atmosphere storage (e.g., nitrogen or CO_2 environments) reduce oxygen availability, thereby limiting lipid peroxidation and enzymatic degradation. Studies in maize and sunflower seeds demonstrate improved longevity under oxygen-limited environments compared to ambient air (Samarah *et al.*, 2013). Silica gel, zeolite beads, and hermetic storage containers have also shown promise in preserving low moisture levels.

Chemical and Antioxidant Priming

Seed priming with antioxidants is a practical approach to enhance defense mechanisms before storage. Antioxidants such as ascorbic acid, glutathione, salicylic acid, and melatonin have been applied to improve ROS-scavenging capacity and maintain membrane stability during storage (Miao *et al.*, 2021). For instance, soybean seeds primed with melatonin exhibited higher germination rates and lower MDA content after accelerated ageing compared to untreated controls (Zhang *et al.*, 2020). Osmopriming and hydropriming, although primarily used for improving germination, have also been found to enhance seed storability by inducing mild stress that activates repair enzymes and antioxidant systems. The use of bio-priming agents like *Trichoderma* spp. and Bacillus subtilis may also bolster defense responses and suppress microbial deterioration during storage (Singh *et al.*, 2021).

Genetic and Molecular Interventions

With advances in plant molecular biology, genetic improvement of seed longevity has become a promising long-term strategy. Several quantitative trait loci (QTLs) associated with storability and ageing tolerance have been identified in crops such as rice, maize, and wheat (Nagel *et al.*, 2009). Genes involved in DNA repair (e.g., LIG1, OGG1), antioxidant enzymes (SOD, CAT, APX), and LEA (Late Embryogenesis Abundant) proteins have been targeted for overexpression in transgenic lines to enhance resilience against ageing-induced damage (Sano *et al.*, 2016). CRISPR-Cas9 genome editing has opened avenues for targeted modifications in key longevity-related genes. For example, manipulating regulators of oxidative stress pathways or chromatin remodeling factors could allow precise control over seed viability under storage conditions. However, regulatory concerns and acceptance issues still limit the widespread deployment of genetically edited seeds.

Use of Nanotechnology

Recent innovations in nanotechnology have led to the development of nanopriming, where seeds are treated with nanoparticles (NPs) such as zinc oxide (ZnO), silicon dioxide (SiO_2), or chitosan-based carriers. These nanoparticles serve dual functions: enhancing water uptake and acting as slow-release carriers for antioxidants or growth stimulants (Kah *et al*., 2018). Studies in tomato and rice have demonstrated improved antioxidant enzyme activity and delayed ageing in nanoprimed seeds. Moreover, nano-encapsulation of antioxidants for controlled release during storage is gaining traction. Such technologies offer exciting potential for seed banks and commercial storage units where long-term preservation is required without repeated interventions.

Biostimulants and Coating Technologies

The application of biostimulants—including seaweed extracts, humic acids, and amino acid formulations—has been shown to improve seed vigor and shelf life by enhancing metabolic readiness and cellular protection (Calvo *et al*., 2014). Seed coatings embedded with antioxidants, antifungal agents, or film-forming polymers also provide physical barriers against oxidative damage and microbial attack during storage (Rai *et al*., 2021). Advanced coating materials like biodegradable polymers and hydrogels can be engineered to release protective compounds gradually, maintaining seed quality over extended periods. These materials are especially relevant in climate-stressed regions with fluctuating storage environments.

Hormonal and Epigenetic Modulation

Phytohormones such as abscisic acid (ABA), gibberellins (GA), and brassinosteroids (BRs) influence seed dormancy, desiccation tolerance, and storability. Pre-storage hormonal treatments or genetic modulation of hormone pathways has shown to delay the loss of viability in several species (Chiwocha *et al*., 2005). Additionally, epigenetic priming—manipulating DNA methylation or histone modification patterns—holds promise in reinforcing chromatin structure and preserving transcriptional competency during ageing (Liu *et al*., 2021).

Conclusion

Seed ageing is an inevitable yet intricately regulated process governed by a multitude of physiological, biochemical, and molecular events that compromise seed viability and vigor over time. As seeds transition through storage, they encounter oxidative stress, membrane disruption, genomic instability, transcriptomic decay, and metabolic imbalances, all of which progressively weaken their regenerative potential. The onset and pace of deterioration are influenced by both internal seed traits and external environmental cues, including temperature, humidity, oxygen levels, and physical integrity. Seeds rich in unsaturated lipids or stored under high-moisture and high-temperature conditions are particularly vulnerable to accelerated deterioration, whereas those harvested at physiological maturity and maintained under controlled storage fare better in longevity. At the molecular level, ageing manifests through DNA and RNA damage, disrupted proteostasis, and epigenetic alterations that impair essential developmental and metabolic pathways. Despite its complexity, significant advances have been made in understanding the mechanistic basis of seed ageing and formulating mitigation strategies. These include conventional approaches like optimized storage conditions and antioxidant priming, as well as frontier technologies such as nanopriming, seed coating innovations, biostimulant treatments, and molecular breeding for longevity traits. Innovations in omics technologies have enabled the identification of biomarkers associated with seed viability loss and have opened avenues for early detection and intervention. While no universal solution exists due to interspecies variability in storage behavior, integrating physiological, molecular, and technological strategies holds the promise of extending seed shelf life and securing agricultural sustainability. As global food security increasingly relies on resilient seed systems, preserving seed quality becomes not merely a post-harvest concern but a strategic imperative embedded across breeding, biotechnology, and conservation programs. Future efforts must focus on refining predictive models of seed ageing, harnessing epigenetic and transcriptional plasticity for enhanced stress tolerance, and translating laboratory insights into scalable solutions for farmers, seed banks, and industry stakeholders. Ultimately, understanding and delaying seed senescence is not just a scientific challenge but a crucial investment in global food resilience.

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