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Biochemical changes during seed deterioration: A review

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Abstract

Seed deterioration is a phenomenon that reduces vigor, viability, and storage, but the rate of decrease differs across crops and genotypes. Crops like Soybean, moringa, rice, and sweet corn show that poor storability results in more oxidative damage, free fatty acids, and malondialdehyde accumulation. Seeds with good storability maintain more antioxidant activity and stable reserve composition. Moringa crop, when harvested at physiological maturity, seeds have reached maximum vigor and storability. Abiotic factors, such as high humidity, in crops like rice, lose longevity at a faster rate, but when seeds are exposed to priming treatment, they have shown better vigour and establishment. Low starch content in sweet corn was especially vulnerable to natural aging, though genotypic variation existed. An imbalance between antioxidant defense and oxidative stress, breakdown of stored reserves, and improper harvest of produce lead to seed deterioration.

Keywords: Seed deterioration, seed ageing, oxidative stress, reactive oxygen species (Ros), antioxidant enzymes, lipid peroxidation, malondialdehyde (Mda), membrane integrity, mitochondrial dysfunction, reserve mobilization and enzyme activity, seed priming

1. Introduction

Seed deterioration and ageing have become a significant threat to the farming communities, reducing the marketing quality of the crops as they age. As a result, there is a reduction in the seed quality parameters such as germination percentage, vigour, and viability of the seed, which disrupts the seed multiplication system of the crop. Seeds, when stored for a period of time, undergo many changes, which may be physical, physiological, or biochemical, acting alone or in combination with one or many. In some cases, Environmental factors such as temperature and moisture serve as key factors for a successful plant establishment, or they may lead to complete deterioration of the seed. As seeds get older, they start collecting harmful substances that slowly damage their protective coat, stored food, and other important parts. One of the warning signs is when MDA levels rise—it shows the seed is under stress and is less likely to grow into a strong, healthy plant. Membrane disruption, loss of reserve proteins and starch, and the breakdown of vital hormones like abscisic acid (ABA) and gibberellins (GA) all contribute to a gradual decline in seed vigor. Notably, the balance between enzymatic and non-enzymatic antioxidants influences how quickly deterioration progresses and whether seeds retain enough vitality for germination. Lipid peroxidation increases with the increase in lipoxygenase activity, which damages cell integrity. The seeds which were deteriorated show significant changes at cellular level, like starch granule breakdown within endosperm, which leads to loss of metabolic reserves. Crops such as sweet corn show better tolerance, lower MDA and LOX activity, and higher activity of antioxidant enzymes and reserve substances. So, identifying and analyzing these changes is crucial for developing practical methods for optimizing the storage environment, selecting resistant genotypes or applying protective treatments that help to preserve seed quality and enhance crop performance in the field.

2. Membrane integrity

The dissolution of the membrane is considered one of the main causes of deteriorating seeds. This damage results from lipid peroxidation, which alters cell permeability, as the interaction of lipids with reactive oxygen species (ROS) produces molecules with varying solubility, including malondialdehyde (MDA). Damage to seed cells results from regular physical conditions and functional loss. During seed ageing, mitochondrial membranes are compromised in vesicles, cristae are shortened, and there is a decline in cytochrome c oxidase, malate dehydrogenase, and NADH levels. These factors render oxidative phosphorylation a less efficient mechanism, resulting in a drop in adenylate energy charge during germination, which ultimately leads to cellular collapse. A study on soybean genotypes found that membrane -dissolving seeds are a primary cause of worsening seeds, as it leads to changes in cell permeability and inability to maintain normal function. Soybean genotypes with poor storers are particularly prone to this damage.

3. Lipid peroxidation

Lipid peroxidation is an important process in seed aging. Lipid peroxidation leads to membrane injury involves formation of hydrogen peroxide through oxidation of unsaturated fatty acids, eventually alters the membrane permeability and disrupts membrane integrity. It consists of interaction between lipids and reactive oxygen species (ROS), which leads to accumulation of compounds such as malondialdehyde (MDA). The imbalance of ROS and antioxidant activity is due to catalyse and ascorbate activity, which reduced the seed aging. The storage capacity of the genotype depends on the malondialdehyde and a sharp accumulation of high lipoxygenase. On the other hand, the low lipoxygenase activity of MDA and low accumulation of MDA, are responsible for making a seed resistant to aging. In soybeans, lipid peroxidation is an important factor in worsening seeds. Researchers found that genotypes with poor storers show a faster accumulation of lipid peroxidation, a sharp accumulation of malondialdehyde (MDA). It is directly associated with loss of seed power. Conversely, good storers with low lipoxygenase activity and MDA reduce accumulation, which helps them resist aging. A study on sweet corn seeds found that natural aging increased the level of lipid peroxidation significantly increased, indicated with high MDA materials. This increase in MDA was associated with germination degree and reduction in the viability of the seed.

4. Oxidative stress

Oxidative stress is the primary factor contributing to seed ageing, oxidative damage, and loss of vigour. This results from an imbalance between the generation and reduction of reactive oxygen species (ROS). A genotypic starvation of soybeans refers to high -filled amino acids, free fatty acids, and malondialdehyde accumulation due to genotype oxidative stress. In the activity of antioxidants relative to excessive ROS production results in cell membrane damage and DNA damage. Research on soybean genotypes indicates that oxidative stress is the primary cause of seed deterioration and loss of vigour. Poor storage soybean varieties exhibit accelerated increases in free amino acids, free fatty acids, and MDA concentration due to this stress. In poorly restored MAUS 61, an imbalance between antioxidants and reactive oxygen species (ROS) occurred due to a diminished supply of antioxidant molecules during oxidative stress, ultimately leading to cellular damage and a decline in seed viability. Damage to oxidative stress is associated with an imbalance between reactive oxygen species (ROS) and antioxidant defense system production.. A study on rice seeds says that a cursor of oxidative stress, accumulation of carbonylated protein, seeds is an important indicator of aging. In sweet corn it was shown that natural aging increases the level of reactive oxygen species (ROS) in the seed. This elevated ROS production is combined with a decline in antioxidant enzymes, causing significant oxidative damage.

5. Antioxidant systems

Antioxidant systems are one of the main processes occurring in seed. Total antioxidant activity can be measured by free radicle scavenging activity. Antioxidant molecules include vitamin E, β-carotene, vitamin C and glutathione. Antioxidants can inhibit the activity of lipid peroxidation by reducing the level of active oxygen species such as super radicals, hydrogen peroxide and hydroxyl radicle by blocking free radical chains. Loss of seed viability is due to reduction in activities of antioxidative enzymes such as SOD, CAT AND GR these play a significant role in providing protection against highly reactive free radicals.

Early indications of seed aging are caused by deficiency of antioxidant enzymes such as antioxidant enzymes or scavenging enzymes such as superoxide dismutase (SOD), Catalase (CAT), ascorbate Peroxidase (APX), and Glutathione Peroxidase (GPX). Superoxide dismutase (SOD) it mollifies superoxide radicals (O°), which are produced during electron transport process, into hydrogen peroxide and oxygen. Whereas catalyse enzyme is important for the removal of toxic H2O2 produced under various stress conditions and therefore, for the avoidance of oxidative stress related damage, by breaking H2O2 to oxygen and water. (Bailly *et al.*, 2002) [10]. Depression of the system is caused by a decrease in scavenging activity, producing ROS. Good storer genotypes, however, do show higher antioxidant enzyme activity due to loss of seed viability. In rice seeds there was an rapid decline in activity of antioxidant enzymes due to the scavenging activity of ROS.

6. Diagnostic biochemical markers

Seed degeneration is marked by permanent metabolic and cellular alterations, including diminished antioxidant ability, loss of reserves, and genetic damage. Therefore, it is essential to investigate the primary deterioration processes occurring in the seed, including the inactivation of antioxidant enzymes, membrane damage, reverse consumption, and genetic damage, to ascertain a comprehensive response to the deterioration mechanisms. The initial occurrence in seed ageing is the reduction of antioxidant enzymes. The antioxidant system comprises enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione peroxidase (GPX), peroxidase (POD), peroxiredoxin (Prx), dehydroascorbate reductase (DHAR), and glutathione reductase. The dysregulation of the antioxidant system results in the formation of reactive oxygen species (ROS), predominantly hydrogen peroxide (H2O2), owing to its comparatively extended half-life (1 ms) relative to other ROS forms (2-4 s), which acts as a significant biomarker for seed degeneration. Reactive oxygen species (ROS) encompass singlet oxygen, superoxide, hydroxyl radicals, and hydrogen peroxide, with certain ROS accumulating during seed ageing. Various soybean cultivars exhibited distinct elevations in H_2O_2 levels from fresh seeds (0 days) to seeds exposed to 9 days of accelerated ageing. Lipid peroxidation is identified as a pivotal event in the ageing process, with oxygen radical-mediated lipid peroxidation and membrane degradation recognised as the principal sources of damage in seed degeneration. Membrane injury is a pivotal occurrence in the seed deterioration process. Lipid peroxidation-induced membrane damage alters cell permeability and results in diminished seed viability. By oxidising unsaturated fatty acids, lipid peroxidation alters membrane permeability and damages structural integrity, compromising membrane integrity and leading to the formation of hydrogen peroxide. Lipidomic acid dehydrogenase (MDA) is the main end product of lipid peroxidation and it shows how damaged and compromised the membranes are from oxidative stress. An important marker of seed deterioration, it is one of the last substances produced by lipid peroxidation. Both hydrogen peroxide and malondialdehyde concentrations were elevated in aged soybean seeds compared to the control group. The concentration of MDA in the cotyledons and hypocotyls of beech (Fagus sylvatica) seeds that were stored for 17 years was five to six times higher than that of seeds that were collected just recently. MDA levels in naturally aged (NA) and artificially aged (AA) seeds of physic nut (Jatropha curcas) were markedly elevated compared to fresh seeds. When three different cultivars of soybean (BMX Raio, BMX Zeus, and DM 53i54) exposed to accelerated aging (0,3,6 and 9 days) results showed varying increase in MDA content. During storage, a good storer of soybean cultivars like Kalitur maintained lowest MDA content among other genotypes MAUS 61 and NRC 93 which shown higher MDA content. Lipid peroxidation disrupts membrane integrity, which leads to leakage of intracellular solutes (like Na+ and K+) including free amino acids, free fatty acids. Therefore, the EC of the seed leachate correlates with membrane damage severity. Seeds subjected to accelerated aging for 14 days showed loss of germination and increased EC compared to control. The EC of physic nut seed soaking solutions also significantly increased after NA and AA treatments During storage, good storer soybean genotypes like Kalitur maintained lower free amino acid (FAA) content, with a 107% increase over 10 months, while poor storers such as MAUS 61 showed a much higher increase of 324%, likely due to greater membrane damage from lipid peroxidation. Similar genotypic differences in FAA content during seed storage was also reported by Salam *et al.*, 2018 [83]. The increase in FFA during storage was also documented by Abreu and it was mainly due to lipid peroxidation. Good storer soybean genotypes also maintained lower free fatty acid (FFA) content during storage, with only a 98% increase, compared to poor storers that showed a 168% increase, indicating greater deterioration in the latter.

7. Reserve mobilization and enzyme activity

The breakdown of starch into soluble sugars by the enzyme alpha-amylase results in enhanced respiration and accelerated seedling growth. Decreased alpha amylase activity is associated with ageing and correlates with suboptimal germination in cereals and rice. Triacylglycerol-stored lipids are mobilised by lipases. Nonetheless, unsaturated fatty acids are susceptible to lipid peroxidation, resulting in the formation of malondialdehyde (MDA), a biomarker indicative of degradation. Genotypes of soybean with elevated oleic acid content demonstrate superior storability compared to those abundant in linoleic and linolenic acids (Silva *et al*, 2023) [28]. Proteins decompose stored proteins into amino acids necessary for the creation of new proteins. The soluble protein percentage significantly affects vigour, with elevated levels associated with seed lifetime. (Silva *et al.*, 2023) [28]. Antioxidant enzymes, including superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione reductase (GR), protect cells from oxidative stress. An attenuation of their activity with age hastens the formation of reactive oxygen species (ROS), resulting in lipid peroxidation, membrane damage, and genetic harm (Ebone *et al*, 2020; Vijaykumar *et al*, 2019) [70, 80].

8. Environmental and genotypic influence

8.1 Environmental factors

Lipid peroxidation and ROS accumulation promoted by presence of high temperature and relative humidity. The storage conditions like aerobic storage which enhances repiration rate and oxidative stress. Storage under vacuum or low relative humidity improves the seed longevity. Addition to these environmental factors, the hormones such as Abscisic acid (ABA), gibberellins (GA) and auxins also contribute with longevity regulation, while ABA often plays a protective role.

8.2 Genotypic variation

The genotypes of soybean, Kalitur and MACS 1416 which are good storers maintains higher antioxidant activity and lower lipid peroxidation, whereas poor storers like MAUS 61 and NRC 93 are most susceptible to deterioration (Vijaykumar *et al*, 2019) [80]. In sweet corn, genotypes with low lipoxygenase activity and reduced MDA accumulation show greater tolerance to natural ageing. In moringa, desiccation tolerance is acquired late in maturation, indicating strong genotype - environment interactions in storability (Gupta *et al*, 2022) [52].

8.3 Gene- Environment interactions

Seed biochemical composition and mineral nutrient status can modulate deterioration. High magnesium levels in soybean enhanced resilience to deterioration, suggesting nutrient- genotype interactions playa a major role in storability. (Ebone *et al*, 2020) [70].

9. Mitochondrial dysfunction and energy decline

The primary energy source for cellular development and metabolism is the mitochondria. Reactive oxygen species (mtROS) production sites and ROS homeostasis are also maintained by them. Superoxide, hydroxyl radicals, and hydrogen peroxide are examples of reactive oxygen species that oxidise cellular components and jeopardise the integrity of the organellar membrane. The superoxide anion (O2−), which also serves as a mediator in oxidative chain reactions, is responsible for the bulk of reactive oxygen species. Apart from NO, O2 − can also produce hydrogen peroxide (H2O2) by reactions with dismutase and other radicals. The reaction result is a potent oxidant called peroxynitrite (ONOO−). Hydrogen peroxide is very harmful because it may freely permeate cell membranes. The respiratory electron transport activity results in the production of MtROS. Complex I and Complex II of the mitochondrial electron transport chain (ETC) are the main sites where mtROS is generated. Due to the presence of ubisemiquinone radicals, ETC, which converts one electron to oxygen to create superoxide, affects the production of ROS. Nevertheless, the relationship between ROS accumulation in the mitochondria of aged seeds and the AOX pathway has not yet been investigated. According to research, succinate dehydrogenase (SDH) has a role in the production of mtROS. Aconitase, an enzyme found in the mitochondrial matrix, converted hydrogen peroxide into hydroxyl radicals during a Fenton reaction with iron and sulphur. To change NADPH into NADP+, NADPH oxidase produces reactive oxygen species in the mitochondria. ROS are created during germination in a number of species, and it is thought that they act as a signal to break the dormant state of seeds. The buildup of ROS causes oxidative damage, malfunction, impairment of the membrane system, and oxidative damage to lipids, proteins, and DNA in the mitochondria. The pyruvate decarboxylase complex, tricarboxylic acid cycle (TCA) enzymes, and ATP synthase subunits are all harmed by oxidative damage to mitochondrial proteins.

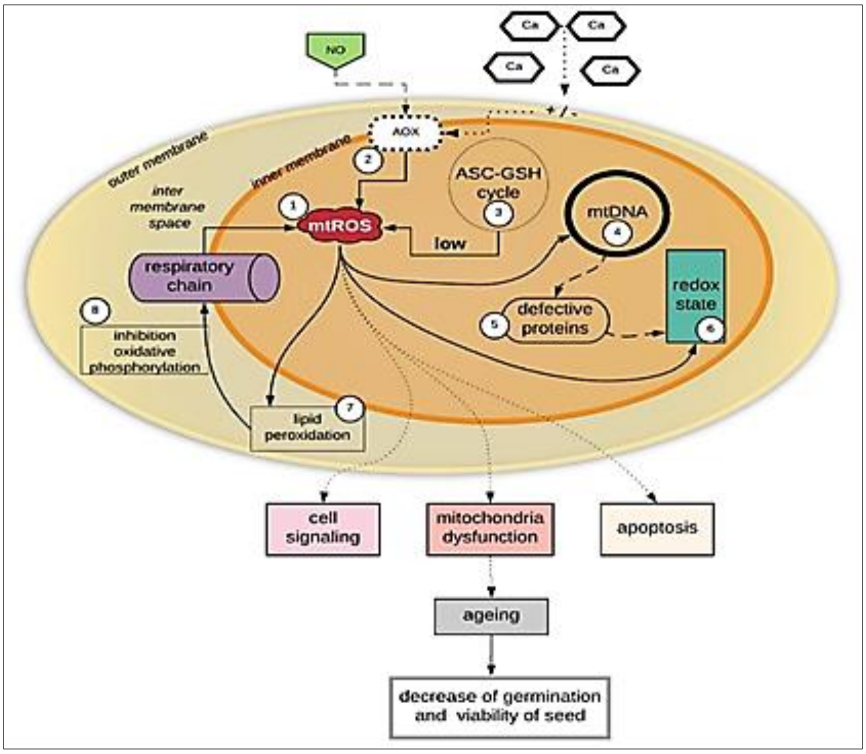

Fig 1: Dysfunctional mitochondria and aging of seeds. Due to continuous reactive oxygen species (ROS) production in mitochondria, the level of ROS increases during seed storage (1).

Nitrogen oxide (NO) influences alternate oxidase (AOX) (2), leading to the formation of reactive oxygen species (ROS) (2). In addition to influencing the rise of ROS levels in mitochondria, calcium ions alter membrane potentials through their interaction with AOX (2). Damage to mitochondrial DNA (4) and protein synthesis (5) due to oxidative stress, as well as alterations in signalling and redox state (6), result from ROS (3) not being properly removed by the ascorbate-glutathione cycle (3). The inhibition of oxidative phosphorylation is affected by oxidative damage to the mitochondrial membranes, which occurs when ROS levels in the mitochondria rise (7). These processes demonstrate the foundation of features of seed ageing and reduce seed viability. As the seeds mature, their viability and germination rates decline, and the processes depicted by the solid arrows are explained by the dotted arrows, which show the roles played by reactive oxygen species (ROS).

The function of mitochondria in the ageing processes of plant seeds remains inadequately characterised. Assessing whether mitochondrial dysfunction simulates seed ageing during storage is crucial. The impact of mitochondrial damage on seed ageing and reduced viability during storage is seen in Figure 1. Although other cellular organelles' antioxidant systems are more effective than the mitochondria's (i.e., the ASA-GSH cycle), the mitochondria's capacity to remove excess reactive oxygen species (ROS) during seed storage is limited. Increased oxidant production and oxidative damage are outcomes of mitochondrial dysfunction caused by ROS. When ROS levels in mitochondria are high, it damages the mitochondrial membrane and makes oxidative phosphorylation more difficult. Mitochondrial DNA can also be oxidatively damaged by reactive oxygen species. Because mitochondrial DNA is located inside the inner mitochondrial membrane, it is more exposed to reactive oxygen species (ROS) and oxidative damage than nuclear DNA, making it a constant target of oxidative stress. Rarely do studies examine mtDNA in plant seeds, in contrast to the vast bulk of ageing studies that concentrate on human cells. Damage to plant seed mtDNA poses a substantial challenge for genome reserve conservation, as compromised genome integrity adversely impacts seed survival. The integrity of mtDNA is contingent upon the generation of mitochondrial reactive oxygen species (mtROS), produced during standard electron flow through mitochondrial electron transport. The protein membrane fails to safeguard mtDNA, and histones are absent from its structure, rendering mtDNA more susceptible to elevated amounts of ROS. In ageing seeds, the accumulation of mtROS inflicts damage on mtDNA and significantly impairs the synthesis of mitochondrial proteins, including those that regulate the mitochondrial redox status, such as peroxyredoxins (Prxs) and thioredoxins (Trxs). The increase of mtROS therefore affects signalling alterations and the redox state of the mitochondria. An elevated concentration of reactive oxygen species (ROS) in the mitochondria induces oxidative damage to membranes, hence impeding oxidative phosphorylation. The cumulative effect of all adverse reactions (1-8) results in a reduction of seed viability (Figure 1).

The expression of genes in both the nucleus and the mitochondria is controlled by the levels of reactive oxygen species in the cell and their redox status. Photosynthesis, stress responses, and programmed cell death are just a few of the many cellular functions that can be impacted by changes in the redox state of mitochondria. As we get older, the second messenger Ca2+ plays a key role in regulating mitochondrial function. In the tricarboxylic acid (TCA) cycle, calcium ions (Ca2+) boost the activity of Ca2+-dependent dehydrogenases, which in turn improves the mitochondrial respiratory chain and, ultimately, the production of ATP by oxidative phosphorylation. The stability of the mitochondrial membrane potential is momentarily compromised by the influx of Ca2+, but this is quickly restored by matrix Ca2+ activating the mitochondrial respiratory chain. When the amount of calcium ions in the mitochondria builds up too much, the inner mitochondrial membrane becomes much more permeable. This causes the mitochondrial membrane potential to drop, respiration to stop, and eventually, pathways that signal cell death to activate. According to Wang and colleagues, the Ca2+ influx could play a role in the AOX retrograde response. According to Xin *et al*., aged seeds are less effective in electron transport chain activities than control seeds, as shown by a decrease in NADH rate, succinate-dependent O2 consumption, and respiration control rate. The efficiency of electron transport chains declines with age, which hinders ATP synthesis and makes it so that old seeds can't produce enough ATP to germinate. Mitochondrial stress causes an energy deprivation signal, which in turn causes extensive changes to gene expression in both the organelles and the nucleus.

10. Ucleic acid damage in seed deterioration

10.1 Nucleic acid damage during seed ageing and deterioration: mechanisms, evidence and implications

Seed deterioration is a complicated and inescapable biological process, characterized by a progressive loss of viability and vigor over time (McDonald, 1999). Though protein oxidation and lipid peroxidation are well recognized as indications of seed aging, multiple study findings point to nucleic acid damage as a critical component regulating seed longevity (Kranner *et al*., 2010; Rajjou & Debeaujon, 2008) [98, 99]. DNA and RNA integrity are essential for germination because they protect genetic stability and aid in the translation of proteins essential for metabolic activity. Nonetheless, the dryness of seeds, along with oxidative stress and poor storage conditions, exposes nucleic acids to various factors that affect their activity.

10.2 Types of nucleic acid damage

Nucleic acids are damaged in various ways during seed storage, which effects seed longevity. DNA is primarily affected by oxidative stress and hydrolytic reactions, which cause strand breaks, a basic site, base modifications such as 8-hydroxy-2′-deoxyguanosine (8- oxo-dG) and DNA-protein crosslinks, all of which impair replication, transcription and repair processes (Bailly, 2004; Cheah & Osborne, 1978) [100, 101]. RNA, in contrast is more unstable due to its single-stranded structure, making it extremely sensitive to fragmentation, ribose oxidation and base changes (Walters, 2015; Fleming *et al*., 2017) [102, 103]. Degradation of stored mRNAs is highly associated with decreased seed vigor because many of these mRNAs code for proteins necessary for germination (Rajjou *et al*., 2004; Basra *et al*., 2003) [104, 105]. Comparative research shows that whereas RNA degrades quickly under storage stress, as shown in soybean and cereal seeds DNA is more robust and frequently shielded by chromatin structure (Ventaka Rao *et al*., 1987; Gomes *et al*., 2019; Cheah & Osborne, 1978) [106, 107, 108,]. According to (Kranner *et al*., 2011) [110], RNA degradation is an early and sensitive indicator of viability loss, whereas DNA damage often happens later in the ageing process.

10.3 Indirect Mechanisms of Nucleic Acid Damage

Nucleic acid damage during seed ageing is also largely caused by indirect methods. As by- products of lipid peroxidation, high levels of malondialdehyde (MDA) and free fatty acids build up in soyabean genotypes that stores poorly. The reactive aldehydes that are produced can covalently bind to DNA bases and hinder DNA repair enzymes like DNA ligase (Gomes *et al*., 2013) [116]. According to Fleming *et al*., (2017) [111], reducing sugars also undergo Maillard reactions with proteins and nucleic acids, producing advanced glycation end products (AGEs) that destabilize RNA, cross link nucleic acids and further impair DNA repair capacity. Furthermore, enzyme imbalances are important because low storability seeds with high lipoxygenase (LOX II) activity encourage the production of hydroperoxides and aldehydes that harm nucleic acids directly or indirectly. In contrast, genotypes with higher antioxidant enzyme activity can limit these oxidative cascades and better maintain genomic integrity (Bailly, 2004; Gomes *et al*., 2013) [100, 116].

10.4 Protective Mechanisms of Nucleic acid Stability

Mechanisms of Nucleic acid stability protection several defence mechanisms found in seeds aid in preserving the integrity of nucleic acids while they are being they are stored. In order to limit the accumulation of reactive oxygen species (ROS) and protect genetic material antioxidant defence systems which include enzymatic antioxidants like superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) and glutathione reductase (GR) as well as non-enzymatic compounds like ascorbic acids, tocopherols, carotenoids and flavonoids are essential. Good storing soyabean genotypes exhibit particularly strong antioxidant activity (Bailly, 2004; Kranner *et al*., 2010; Gomes *et al*., 2013) [100, 98, 116]. Furthermore, as demonstrated in Moringa oleifera seeds, where the accumulation of non- reducing sugars such as sucrose and raffinose-family oligosaccharides create a cytoplasmic glassy matrix that prevents oxidative and hydrolytic damage, dessication tolerance also helps to protect nucleic acids. Furthermore, late embryogenesis abundant (LEA) help to stabilize nucleic acids during dehydration (Hoekstra *et al*., 2001; Hundertmark & Hincha, 2008) [112, 113]. Seed life also influenced by mineral nutrition, magnesium increases storability by reducing oxygen transport, improving membrane stability and indirectly reducing ROS formation, providing nucleic acids with more protection.

10.5Comparative Insights across Plant Systems

Studies on soybeans studies shows that RNA degradation limits germination, more than DNA damage and that RNA stability is directly related to seed viability. While poor storers accumulate aldehydes and lose enzymatic protection. Excellent storers preserves antioxidant defences (Gomes *et al*., 2013) [116]. As an example of how strategies techniques might jeopardize nucleic acid stability, seed priming in rice increases vigor and germination but predisposes seeds to nucleic acid oxidation and poor DNA repair (Kranner *et al*., 2011) [110].

Seed deterioration of nucleic acids is a major cause of seed ageing. While RNA is more delicate and degrades more quickly than DNA it is more susceptible to oxidative and aldehyde-induced damage as antioxidant defences wane (Gomes *et al*., 2013; Kranner *et al*., 2011) [116, 110]. Although reactive functions across species are still unclear, protective mechanisms that protect nucleic acids include enzymatic and non-enzymatic antioxidants, non-reducing sugars, late embryogenesis abundant (LEA) proteins and mineral balance (Bailly, 2004) [100].

11.Practical approaches to overcome seed deterioration, improve seed performance and its longevity

11.1Seed Priming

The storage of orthodox seeds under low-temperature, dry, and oxygen-free conditions can effectively delay seed deterioration, while seed priming technology can restore the vigor of aged seeds. Seed priming is a controlled hydration technique where seeds are partly hydrated to allow metabolic events to occur without germination and are then re-dried to permit routine handling (Bradford, 1986) [85]. Seed priming enables seeds to complete preparatory processes for germination, such as enzyme activation, DNA repair, and membrane system restoration, promoting rapid and synchronized germination under favorable conditions. This enhances seedling emergence and establishment rates (Paparella 2015) [86]. Primed seeds usually have higher and synchronized germination (Farooq *et al*., 2009) [91] owing to simply a reduction in the lag time of imbibition taking place, build-up of germination-enhancing metabolites (Farooq *et al*., 2006) [93], metabolic repair during imbibition and osmotic adjustment (Bradford, 1986) [85]. Priming of seeds has been reported to reverse some of the aging-induced deteriorative events and thus improve seed performance (Taylor *et al*., 1998) [94] through repairing the age-related cellular and sub-cellular damage (proteins, RNA, and DNA) of low-vigor seeds that might have accumulated during seed development (Koehler *et al*., 1997) [95]. Many seed priming treatments have been used to reduce the damage of aging and improve their performance in many crops (Farooq *et al*., 2009) [91]. Current seed priming methods are hydro-priming, osmo-priming, chemo-priming, solid-matrix priming, phytohormonal priming, bio-priming, nutrition- priming, nano-priming, and physical priming. Every technique has unique benefits: Although water priming is inexpensive and pollution-free, it could cause uneven germination; Osmotic priming successfully stops severely degraded seeds from germinating too soon; Solid-matrix priming supplies nutrients and regulates the development environment; Plant hormone priming improves antioxidant defences and is more effective at repair than water priming; Microbial metabolites are used in biological priming to preserve membrane integrity, repair damaged membranes, and lessen electrolyte leakage; Through the use of nanoparticles, nano-priming reduces lipid peroxidation, activates antioxidant mechanisms, neutralises ROS through surface-active sites, penetrates seed coats, and delivers trace nutrients to embryos. Osmopriming in safflower (*Carthamus tinctorius* L.) with CaCl2 for 6h improved antioxidant enzyme activity and germination rate.When soybean (Glycine max L.) is subjected to hormone priming using SA hormone for 8h, an increase in enzyme activity and a reduction in malondialdehyde (MDA) content are observed.(Nazari *et al* 2020) [88]. Bio- priming, which integrates beneficial microbes like the novel strain SH-8, activates systemic resistance and nutrient solubilization, improving drought tolerance by 20% in wheat.

11.2 Addition of plant growth regulators

The exogenous application of plant growth regulators like GA3, Kinetin, ABA, and Indole-3- butyric acid prior to storage has been found to retard seed deterioration and maintain seed vigor and germination (Choudhury *et al*, 2023) [90].

11.

12. Conclusion

Seed deterioration is a complex process that depends on biochemical changes such as lipid peroxidation, oxidative stress and loss of antioxidant defences which together damage membrane integrity, energy production and genomic stability, ultimately resulting in loss of seed viability and vigor. These mechanisms have been observed in some diverse crops such as soybean, rice, sweetcorn and moringa, highlighting the challenges in maintaining seed quality during storage and ageing. Biochemical indicators like antioxidant enzyme decline, malondialdehyde accumulation provide critical results for minimizing seed deterioration. So, practical approaches such as controlled storage conditions, seed priming and application of plant growth regulators have shown minor detrimental changes. However, the results differ based on genotype and treatment method. In summary, knowledge of biochemical pathways clarifies the mechanisms underlying seed aging and enables implementation of specialized strategies to maintain seed viability and improve storage life.

Disclaimer (artificial intelligence)

The author(s) hereby declare they have not used generative AI technologies such as Large Language Models (Chat GPT, COPILOT, etc.) and text-to-image generators while writing or editing manuscripts.

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Competing interests

The author (s) declared that no conflict of interest exists.

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