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CONCEPT OF SEED DETERIORATION: REASON, FACTORS, CHANGES DURING DETERIORATION AND PREVENTIVE MEASURES TO OVERCOME SEED DEGRADATION

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ABSTRACT

Seed deterioration is when a seed loses its vigor and eventually loses viability. Seed viability is an important trait that directly influences seedling emergence and crop yield. The rate of seed deterioration varies on several factors. Our main aims were to express the methods for testing seed deterioration, factors influencing seed aging, stages of seed deterioration, changes associated with seed deterioration, Practical approaches to overcome seed deterioration, and the role of reactive oxygen species during seed aging. From this investigation, it can be concluded that high temperatures and high relative humidity can hasten the degradation of seeds. An increase in the loss of seed leachate, a drop in respiration rates and ATP production, a loss of enzyme activity, and organelle structural breakdown are often seen as changes as seeds age. Various factors can cause seed aging, but the main cause is probably oxidative damage brought on by free radicals and reactive oxygen species (ROS). Protein oxidation, lipid peroxidation, chromosomal abnormalities, and DNA damage can all be induced by ROS, which can have critical interactions with any macromolecule of biological significance. In the early stages of imbibition, some repairs may occur, and seeds will lose their viability within a short period. Seed deterioration can be retrieved through different priming and exogenous application of plant growth regulators.

INTRODUCTION

Seed deterioration means the loss of viability and vigor due to the effect of aging as well as adverse environmental factors, particularly higher temperature, relative air humidity, and oxygen/carbon dioxide ratio during pre-harvest (field weathering), harvest (handling) and post-harvest (storage) periods (Kapoor et al., 2010; Farhadi et al., 2012). It also refers to deteriorative changes occurring with time that increase the seed's vulnerability to external challenges and decrease the ability of the seed to survive. When a seed is exposed to more external stressors, degenerative changes become more pronounced and reduce the seed's capacity for survival. According to Kapoor et al. (2011), the process is cumulative, irreversible, degenerative, and inexorable. For many commercially produced crops in agriculture, seeds are a fundamental form of plant propagation.

Furthermore, seeds can be the main focus of initiatives aimed at environmental restoration and help ensure the long-term maintenance of genetic diversity (Baskin & Baskin, 2020). All seeds will eventually lose their viability as they age and perish, a process known as seed degeneration or aging (Ebone et al., 2019), even when stored under ideal conditions. It has been estimated that 25% of seeds lose their viability annually, which can give rise to billions of dollars of economic losses (McDonald & Nelson, 1986). Seed aging can be described as irreversible, cumulative, and inexorable (McDonald, 1999). As a result, the emergence of seedlings may be delayed, and their ability to withstand environmental stress during germination and the early stages of growth may be reduced. The delay in germination in somewhat old seeds is connected to the ability of seeds to make certain repairs during the early stages of imbibition (Xu et al., 2020; Kumari et al., 2017). However, substantial damage would eventually exceed a seed's capacity to heal itself as it ages, and the seed would lose its

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ability to be viable (Bewley et al., 2013; Ray & Bordolui, 2022). In general, cool, dry storage can extend the viability of stored orthodox seeds, whereas high temperatures and high relative humidity can hasten the deterioration of seeds (Ellis & Hong, 2006). The research on seed aging has been conducted using two broad methods. In the first, seeds are stored for several years under natural conditions. However, because this requires a long time to reveal changes in the seeds, artificial aging conditions can also be used, such as several days of storage at high temperatures and high relative humidity (Pournik et al., 2019); such treatment is also referred to as 'accelerated aging' or 'controlled deterioration treatment' which could simulate the biochemical and molecular events taking place during the natural aging of seeds (Rajjouet al., 2008). Our comprehension of seed aging has substantially benefited from the studies conducted by numerous authors. According to some research, a number of processes, including lipid peroxidation (Oenel et al., 2017), protein carbonylation (Rajjou et al., 2008; Li et al., 2017), and programmed cell death (Hu et al., 2012), are causally linked to the degeneration of seeds. On the other hand, aging denotes a complex biological phenomenon linked to various biochemical, molecular, metabolic, and physiological processes (Ebone et al., 2019). However, the primary objectives of this review are to know (1) methods for testing seed deterioration, (2) factors influencing seed aging; (3) stages of seed deterioration, (4) changes associated with seed deterioration; (5) the roles of reactive oxygen species during seed aging and (6) practical approaches to overcome seed deterioration

The quality of seed can be determined by several factors during the product phase in the field before harvesting, during harvesting, threshing, drying, cleaning, grading, packaging, storehouse, transport, and sowing. These factors include extreme temperatures during development, changes in humidity conditions including failure and redundant rains at development, riding, factory nutrition scarcities, circumstance of pests and conditions, indecorous running, drying, and storehouse (Cavatassi et al., 2010). Seed aging or deterioration is a natural process that results from the commerce of cytological, physiological, biochemical, and physical changes in seed, causing a reduction in vigor and germination and ultimately leading to the loss of viability. Thus, testing the quality of seeds stored for different lengths of time is important to determine the effect of aging on seed quality (Finch-Savage & Bassel, 2016). Seed deterioration is to be retrieved by different seed treatments before storing and mid-term storing.

LITERATURE REVIEW

Ranganathan and Groot (2023) reported that the basic deterioration processes that lead to a drop in seed viability contrastingly vary between desiccation asleep (orthodox) and desiccation-sensitive seeds (recalcitrant). Orthodox seeds which suffer development drying are bestowed with defensive mechanisms which guard the seeds against deterioration. They include the accumulation of antioxidants, non-reducing sugars, defensive proteins similar to late embryogenesis abundant proteins, heat-shock proteins, lipocalins, hormones, and chemical protectants (raffinose family oligosaccharides, flavonoids, lignins, vitamin E). The nuclear DNA is packed thick, and chlorophyll is degraded. Still, with low humidity content and a glassy state of cytoplasm, reactive oxygen species generated due to the presence of oxygen in the storehouse atmosphere may beget the aging of the seed. As the seed humidity content increases, mitochondrial respiration gets activated, leading to an increased product of reactive oxygen species owing to hamstrung mitochondrial exertion. The reactive oxygen species lead to the oxidation of essential motes similar to DNA, RNA, proteins, and lipids.

Further, mitochondrial membranes also oxidize, reducing aerobic respiration eventuality. When the damage is not substantial, orthodox seeds can repair the molecular damages accumulated during storehousing, enabling the seeds to overcome the damages and extend their life incompletely. This includes activating cell membranes, DNA, RNA, proteins, and mitochondria as the seeds imbibe water.

Zhang et al. (2021) suggested that during seed aging, constantly observed changes include membrane damage and the destruction of organelle structure, an increase in the loss of seed leachate, diminishments of respiratory rates and ATP product, and a loss of enzymatic exertion. These marvels could be interrelated and reflect the general breakdown in the cellular association. Numerous processes can affect seed aging; likely, oxidative damage caused by free revolutionaries and reactive oxygen species (ROS) is primarily responsible. ROS can have vital relations with any macromolecule of natural interest that affect damage to colorful cellular factors caused by protein damage, lipid peroxidation, chromosomal abnormalities, and DNA lesions. Further, ROS may also beget programmed cell death by converting the opening of mitochondrial permeability transition pores and the release of cytochrome C. Some repairs can do in the early stages of imbibition, but form processes fail if sufficient damage has been caused to critical functional factors. As a result, a given seed will lose its viability and ultimately fail to germinate fairly quickly.

MATERIALS AND METHODS

Seed vigor tests are designed to determine how the seed lot will perform under stress. It is the opposite of a germination test, where the seed is grown under optimum conditions. As a consequence, there are various techniques to determine its assessment, including those that directly or indirectly evaluate the current seed metabolic state to establish a relationship with seedling emergence and storability; those tests include (i) electrical conductivity, (ii) tetrazolium, (iii) vital coloring test (iv) Enzyme activity test (v) X-ray photography test (vi) ferric chloride test (vii) Accelerated Ageing (viii) cold test and (ix) germination test that evaluate the seed deterioration.

Electric Conductivity

Electrical Conductivity (EC) is a promising vigor test classified as a biochemical test. EC test aims to indirectly evaluate the extent of damage caused to cell membranes resulting from seed deterioration (Mohammadi et al., 2011). The genotype, seed integrity, size, moisture content, soaking period, and temperature affect electrical conductivity results (De Carvalho et al., 2009). The EC is based on the fact that seeds, when soaked in water, exude ions, sugars, and other metabolites, from the

start of the soaking period, due to changes in the integrity of the cell membranes, as a function of the water amount and of the level of seed deterioration. In deteriorated seeds, the repair mechanism is absent or inefficient, or the membranes are completely damaged, thus permitting the leaching of larger electrolyte amounts.

A seed ample of 2-5 grams is weighed and surface sterilized with 0.1% $HgCl_2$ for 5-10 minutes. The sample is washed thoroughly in distilled water. The clean seeds are immersed in 100 ml water at 25±1°C for 10-12 hours. After this, the seeds are removed with clean forceps. The steep water left is decanted and is termed leachate.

The conductivity meter is warmed for about 30 minutes before testing. First, the conductance of distilled water is measured in a beaker. The electrode is then cleaned with tissue paper, and the conductance of the leachate is read. The electrode is thoroughly washed using a wash bottle and wiped with clean tissue paper before reusing. While recording the conductance, the lower bulb of the electrode should be fully immersed in the leachate. To get the leachate's EC, the distilled water reading is subtracted from the sample reading. The value is then corrected for the temperature and multiplied by the cell constant factor. The reading is expressed as mS m^{-1} of seed. The lower the value of EC, the greater the seed vigor.

Figure 1. Assessing the efficiency of electrical conductivity (EC) test

Tetrazolium Test

The Tetrazolium Chloride (TZ) test is considered the quick germination test. The TZ test can give an early and quick snapshot of seed viability but still needs to replace the more comprehensive seed germination test (Vermaet al., 2013). The test is useful for processing, handling, storing, and marketing. Large quantities of seed in a short time, testing dormant seed lots, vigor rating of the seed lots, and diagnosing the cause of seed deterioration. TZ is a biochemical test that differentiates live from dead seeds based on the activity of the respiration enzymes in seeds. Upon seed hydration, the activity of dehydrogenase enzymes increases, resulting in the release of hydrogen ions, which reduces the colorless tetrazolium salt solution (2, 3, 5-triphenyl tetrazolium chloride) into a chemical compound called formazan. Formazan stains living cells (respiring) red, while dead cells (not respiring) remain colorless. The viability of seeds is interpreted according to the staining pattern of seed tissues (Filho, 2015).

Figure 2. Viable seeds turn into red color

$$\text{Viability \%} = \frac{\text{Number of red-stained seeds}}{\text{Total number}} \times 100$$

Vital coloring test

The principle of this method is the differential coloration of life against dead tissue when exhibited to such dyes as sulphuric acid, indigo carmine, and aniline dyes. These dyes stain the dead tissue and the live tissue leftovers unstained. This method is particularly useful for determining the viability of tree seeds.

Enzyme activity test

These methods measure enzyme activity (such as lipase, amylase, diastase, catalase, peroxidase, and dehydrogenase) of imbibed seeds to indicate their viability.

X-ray photography test

This is generally used to test the viability of forest seeds. $BaCl_2$ penetrates the dead cells but does not penetrate the living cells because of their semi-permeability. Thus dead parts of the embryo and endosperm are contrast areas in X-ray photography.

Steps: Soak the seeds in water for 16hrs. → Drain excess water → soak 20% to 30% $BaCl_2$ for an hour → after drying, seeds are radiographed using soft X-rays.

Ferric chloride test

Mechanically injured areas of legume seeds turn black when placed in the ferric chloride solution. A ferric chloride ($FeCl_3$) solution is prepared by adding four parts water to one part $FeCl_3$. Two replicates in a petri-dish, each 100 seeds, are commonly immersed in the $FeCl_3$ solution. After five minutes, black staining seeds exhibiting mechanical damage are separated from those remaining seeds.

Accelerated Ageing

Accelerated aging is a technique of seed vigor testing initially developed for testing the storage potential of seeds. Subsequently, the test has been evaluated to indicate seed vigor in various crops (Powell & Matthews, 1981). The principle of the method is based on the artificial acceleration of the deterioration rate of the seeds by exposing them to high temperature (40 to 45^0C) and relative humidity (greater than 95%) levels (TeKrony, 2005), which are considered the most prominent environmental factors for the intensity and velocity of deterioration. In this situation, low-quality seeds deteriorate more rapidly than vigorous ones, presenting a differentiated decrease in viability. An environment of 41 to 43^0C temperature for 24 to 72 h is considered applicable for many species in AA (Hampton et al., 1992; Matthews, 1993).

Figure 3. The accelerated aging technique of the seed vigor test

Cold test

It was developed to evaluate the physiological potential of corn seeds, seeking to stimulate adverse soil conditions (excessive water, low temperatures, and presence of fungi in the soil) that frequently occur during the sowing season in the US Corn Belt. Loeffler et al. (1985) suggested another procedure by using a germination paper towel without soil, known as the cold test without soil. This procedure was sensitive enough to detect drying damage in corn seeds and provide greater reproducibility of results due to the simplicity of the method. Therefore, the cold test seeks to evaluate the effects of a combination of low temperature, microorganism action, and high substrate moisture by identifying differences in physiological potential among seed lots (Caseiro & Marcos- Filho, 2002).

Germination Test

It is an analytical procedure to evaluate seed germination under standardized favorable conditions. Standard germination testing includes temperature, moisture, light, dormancy breaking, and germination counting standard of seeds.

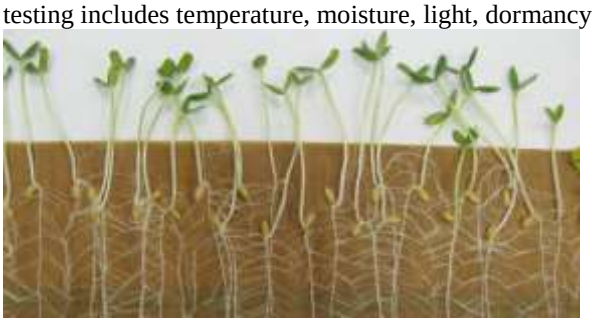

Figure 4. Seedlings after germination

$$\text{Germination \%} = \frac{\text{Numbers normal seedlings}}{\text{Total}} \times 100$$

RESULTS AND DISCUSSIONS

Results of Factors Influencing Seed Ageing

Genetic factors

Genetic factors undoubtedly influence seed quality. Seeds from various genera, species, cultivars, or individual plants frequently exhibit variances in their ability to be stored under the same conditions (Raoet al., 2017). Some seeds, such as Lactuca sativa and Allium cepa, have a limited shelf life by nature. In contrast, Pisium sativum and Triticum aestivum seeds have a substantially longer shelf life when kept in the right storage circumstances (Mira et al., 2015). Eighteen crop species were stored dry at room temperature and 50.5% relative humidity for 1-26 years, and Nagel and Borner (2010) compared the germination/viability of the crops. According to Nagel and Borner (2010), it took all seeds five to seven years to lose their viability, but it took Phaseolus vulgaris and Vicia sativa more than twenty years. These species-specific variations have been linked to some biochemical factors, including the concentrations of tocopherols, lipocalins, and antioxidant polyphenols, positively correlated with seed storage behaviors (Sano et al., 2016).

Additionally, it has been noted that seeds with physical dormancy, such as several species of the Fabaceae and Nelumbonaceae, typically have a longer lifespan than seeds of other species (Baskin & Baskin, 2020). Nelumbo nucifera seeds, for instance, have been found to endure for 1300 years (Copeland & McDonald, 2012). This species-specific genetic variable associated with the outer seed coat's resistance to gases and liquids may also help maintain seed viability (Harrington, 1972).

Maturational and harvest conditions

Seed viability is influenced by seed maturity during harvest or shedding (Rao et al., 2017). In the same seed lot, mature seeds withstand storage far better than immature seeds (Copeland & McDonald, 2012). However, delayed harvest can also cause the aging process to occur in the field, especially when there is a high seed moisture content, which reduces the viability of subsequent storage (Bewley et al., 2013). The most suitable time for storage is after seeds have attained physiological maturity or have reached their maximum dry weight.

Relative humidity and temperature

The two environmental factors that directly impact seed degeneration are relative humidity (RH) and temperature (Rajjou et al., 2008). The level of water vapor surrounding the seeds and the moisture content of the seeds are in equilibrium throughout storage. Hence the RH has a direct impact on this. According to Copeland and McDonald (2012) and Baskin and Baskin (2020), the real seed moisture content during dry storage is typically 5–10%. According to Rao et al. (2017), an increase in relative humidity causes an increase in seed moisture content, which in turn causes an increase in seed aging. According to Harrington (1972), seed viability was maintained at a 5-14% moisture level. However, for every 1% rise in seed moisture content above 14%, seed viability falls by 50%. When a seed's moisture content exceeds 14%, respiration is accelerated, and fungi speed up the loss of seed viability (Ellis & Hong, 2006). Although, seeds may develop a glassy condition when their moisture content falls below 6%, giving their cytoplasm a high viscosity and low molecular mobility, which inhibits enzymatic metabolism (Murthy et al., 2003). The viability of seeds decreased as the storage temperature increased, even when seeds were kept at low moisture content. According to Hartmann-Filho et al. (2016), rising temperatures speed up chemical reactions in seeds, which starts the early phases of seed degeneration. In addition, even when the relative humidity is kept constant, warmer air offers the seed more readily available water than cold air (Copeland & McDonald, 2012). Harrington (1972) also reported that seed viability decreased by 50% for each 5^0C to increase the temperature range of 0–50 ◦C. When temperatures fall below 0^0C, some biochemical reactions related to the deterioration of seeds will not occur, and an additional temperature decrease will moderately affect seed viability extension (Harrington, 1972).

Discussions of Different Stages of Seed Deterioration

Various stages and factors affecting Seed deterioration: Generally, seed deterioration pattern is taken into consideration in three stages, i.e. (a) During the pre-harvest or field weathering stage, (b) during the Harvesting and Post-harvest stage, and (c) During the storage period.

Pre-harvest or field weathering stage

The physiological quality of seeds depends on the weather conditions before harvesting (Padua et al., 2009). Field weathering is called seed quality, vigor, and viability deterioration due to high relative humidity and high temperature during the post-maturation and pre-harvest periods (Bhatia et al., 2010). The period between the physiological maturity of the crop and harvesting is considered weather-prone. High rainfall, elevated temperature, R.H., and prolonged photoperiod are pre-harvest factors that cause seed quality loss following physiological maturity. However, moisture on seeds during ripening appears to exert a major influence on the predisposition of seeds to weathering. Adverse environmental conditions during

seed filling and maturation result in forced seed maturation, associated with low yields, leading to a significant decrease in quality and an extensive reduction in crop productivity (Padua et al., 2009). After physiological maturity, if the seeds are retained on the mother plant, seeds will deteriorate, and physiological changes in the seed may lead to the formation of rigid or colored seeds (Khatun et al., 2009). Delayed harvesting beyond physiological maturity and exposure to field weather further aggravates the loss of seed quality. Weathering-induced seed damage lowers the seed germ's inability and becomes prone to mechanical damage and infection.

Seed deterioration during harvesting and post-harvesting stage

Harvest and post-harvest handling of seeds include harvesting, threshing, machinery processing, seed collection, storing, transporting, drying, and marketing which greatly influences seed quality and viability. Better seed quality may only be achieved if proper post-harvest handling is performed. Over-drying of seeds increases the chance of mechanical damage and injuries in the form of physical damage or fracturing of essential seed parts. Physical seed damage is also exhibited as the splitting of the cotyledon and shattered and broken seeds. Broken seed coats permit early entry and easy access for harmful microflora, making the seed vulnerable to fungal attack and reducing storage potential (Shelar, 2008).

Deterioration during the Storage period

The storability of seeds is mainly a genetically regulated character. It is influenced by the quality of the seed at the time of storage, the pre-storage history of the seed (environmental factors during pre- and post-harvest stages), moisture content of seed or ambient relative humidity, the temperature of the storage environment, duration of storage and biotic agents (Khatun et al., 2009; Chakraborty et al., 2020). Storage life of seeds doubled with each 1% (within 5 to 14% seed moisture content) reduction in seed moisture or each 5ºC (within 0 to 50 ºC) reduction in temperature (Harrington, 1972). The seeds rich in lipids have limited longevity due to their specific chemical composition, leading to loss of germination ability and viability. The main external factors causing seed deterioration during storage are high temperature, R.H., and O_2/CO_2 concentration, which increase the respiration rate causing seeds to deteriorate more rapidly (Kapoor et al., 2010) and therefore, the possibility of regulating these factors makes the basis for longer seed storage (Mohammadi et al., 2011; Ray & Bordolui, 2020). However, these environmental conditions are very difficult to maintain during storage, and damage to seed during storage is inevitable (Balesevic-Tubic et al., 2005).

Discussions of Changes Associated with Seed Deterioration like Morphological Changes, Ultra Structural Changes, Biochemical Changes, Genetic Changes, and Physiological Changes

Morphological changes

A change in seed coat color is observed in deteriorated seeds. Darkening of the seed coat in deteriorating clover, groundnut, and soybean seeds have been reported. Such color changes are presumably due to oxidative reactions in the seed coat, accelerated under high temperature and relative humidity conditions. Alterations in seed morphology frequently occur together with seed aging. As seen in Brassica napus and Linum usitatissimum (Sano et al., 2016), the color of the seed coat can indicate the degree of seed degradation. According to Copeland and McDonald (2012), the seed coats of degrading seeds of Arachis hypogaea, Glycine max, and three different Trifolium spp. have darkened. Researchers have noted additional morphological changes in old seeds in addition to the impact on the seed coat. After five years of storage, nonviable seeds of Citrullus lanatus and Cucumis melo showed a considerable rise in internal air space, and each nonviable seed carried a tiny, typically formed embryo (Ahmed et al., 2019).

Ultra-structural changes

After being stored or after accelerated aging, seeds lose their ability to germinate, and this is related to structural changes in different organelles (Smith & Berjak, 1995). According to reports, the first organelles to sustain damage during seed aging are the mitochondria, the site of cellular energy synthesis and material metabolism (Wang et al., 2012). The outer membrane and cristae of aged embryos' mitochondria are noticeably distorted during seed aging, from becoming disorganized to virtually missing (Bailly, 2004). Wang et al. (2015) classified the mitochondria of Ulmuspumila seeds into four types: punctiform, vermiform, gigantic, and diffuse. Numerous punctiform mitochondria were consistently distributed throughout the cytoplasm of young seeds. The mitochondria grew longer and grouped as the seed grew older. The mitochondria accumulated on the cell membrane and dispersed as seeds lost viability (Wang et al., 2015). Smith and Berjak (1995) specified additional ultra-structural alterations, aside from mitochondria, that are consistently linked to seed aging. These alterations include Golgi bodies and endoplasmic reticulum fragmentation or disappearance, lipid droplets fusing to form larger or irregular bodies, the membranes of protein bodies and vacuoles dissolving, the plasma membrane deteriorating and contracting away from the cell wall, and disintegration. The process of seed deterioration could be responsible for following ultra-structural changes in the seed.

Cell membranes

- Withdrawal of plasma lemma and coalescence of lipid bodies influence cell membrane integrity.
- Formation of free radical.
- Loss of cell membrane integrity.
- Leads to the release of different seed leachates.

Mitochondria

- Mitochondria become permanently swollen and lose their natural swelling contracting ability.
- Reduction of dehydrogenase activity.
- Hampered in NADH and FADH enzyme formation.
- Ultimately formations of ATP become hampered.
- It leads to loss of function and eventual fragmentation.
- Decrease in the respiration rates of seeds.

Ribosomes

- Associated with degradation of function in deteriorating seeds in the dissociation of the ribosome.
- Evidence indicates that the dissociation of polyribosomes occurs before the attachment of performed mRNA occurs, leading to protein synthesis in germinating seeds.
- Protein synthesis retarded.

Biochemical changes

Some important enzymes, such as those involved in ATP generation, amylase, cytochrome c oxidase, carboxylase, dehydrogenases, DNA polymerase, DNA ligase, esterase, lipoxygenase, phosphatases, proteinases, and proteases, are rendered inactive as seeds degenerate (Walters & Engels, 1998). As enzyme activity declines, this can diminish seed respiratory potential, affecting the synthesis of ATP and the amount of food available to the sprouting seed (Xin et al., 2014). The seed's overall degree of metabolic activity is reflected in the respiratory rate. The respiratory quotient (RQ), which measures the amount of CO_2 produced as the seed uses oxygen, maybe a reasonably sensitive indicator of degradation. In degraded seeds, a relatively high RQ (1.5 or higher) has been observed, possibly due to increased CO_2 evolution, decreased oxygen consumption, or both (Wang et al., 2014).

Seed deterioration has been attributed to various biophysical and biochemical changes in seed components, such as the loss of enzymatic activities, the loss of membrane integrity, the accumulation of toxic substances, and genetic alterations.

Loss of enzyme activity

- The breakdown of food reserves occurs due to the biosynthesis of new tissue during germination.
- Various critical enzymes are inactivated when seeds deteriorate, such as ATP synthesis, amylase, cytochrome-oxidase, carboxylase, dehydrogenases, DNA polymerase, DNA ligase, esterase, lipoxygenase, phosphatases, proteinases, protease, which have been correlated with seed deterioration (Walters & Engels, 1998).

Reduced respiration

- Respiration is associated with the breaking down food reserves by a large group of enzymes.
- As seeds deteriorate, respiration becomes progressively weaker, ultimately leading to germination loss.
- The RQ (respiratory quotient) value of deteriorated seed is high due to more CO_2 release and less uptake of O_2.

Lipid peroxidation

- Lipid peroxidation refers to the oxidative degradation of lipids. It is the process whereby free radicals steal electrons from the lipids in cell membranes, resulting in cell damage.
- Lipid peroxidation and associated free radical oxidative stresses are considered to be major contributors to seed deterioration.
- Loss of membrane structure and increased leakiness of oxygen is responsible for damaging plant tissues in inhibiting chloroplast development, seed viability, and root growth.

Degradation of food reserves:

- Studies with radioactive amino acids in many seed species have shown that seed deterioration is associated with reduced capacity for protein synthesis (Anderson, 1977).
- Parallely, the amylase activity is also increased. A sharp decrease in protein content in aged seeds of maize will lead to a drastic increase in the total free amino acids. Similarly, lipid content also decreased.

Genetic changes

Seed quality is dependent on genetic factors. Under the same storage conditions, seeds of different genera, species, cultivars, or individual plants often show differences in their storability (Rao et al., 2017). The process of seed deterioration could be related to the following genetical changes-

- Slower seedling growth.
- DNA is degraded and fails to produce mRNA, which results in no enzyme formation causing a reduction in germination.
- During storage, stored mRNA may be degraded, which ultimately causes seed deterioration.

Physiological changes

The process of seed deterioration could be associated with the following physiological changes-

- Delayed germination.
- Increase in abnormal seedlings.
- Reduce the speed of germination.
- Low vigor index.
- Reduced seedling growth.

Discussions on the Role of Reactive Oxygen Species (ROS) During Seed Ageing

Production of reactive oxygen species (ROS) and breakdown of antioxidative systems

Reactive oxygen species is one of the by-products of aerobic respiration (Bailly, 2004). Low levels of ROS in seeds act as crucial signal molecules for seed germination, dormancy reduction, and pathogen defense (Apel & Hirt, 2004). However, if seeds are stored for a lengthy period or under improper settings, ROS levels may cumulatively rise (Bailly, 2004). The most significant element influencing seed aging has typically been an increase in ROS; ROS causes oxidative damage to lipids, proteins, and DNA, finally resulting in a loss of viability (Waszczak et al., 2018). The primary source of ROS is the mitochondrial respiratory electron-transport chain (ETC), specifically complexes I and III (Fig. 1). According to Moller et al. (2020), superoxide radicals are created as a result of electron leakage in the transport chain. These radicals are then effortlessly transformed into hydrogen peroxide (H_2O_2) by mitochondrial SOD. Finally, hydroxyl radicals (OH), which are extremely active and poisonous, are created when transitional metals combine with H_2O_2 in the Fenton or Haber-Weiss reactions (Imlay, 2003). Furthermore, in dry seeds with low metabolic and enzymatic activity, the auto-oxidation of lipids produces ROS, which is then trapped inside the seed tissues (McDonald, 1999). To battle these free radicals and neutralize their negative effects, aging seeds have evolved a variety of defensive mechanisms or antioxidative systems (Fig. 1). CAT, SOD, guaiacol peroxidase (GPx), ascorbate-glutathione (AsA-GSH) cycles of enzymes, as well as nonenzymatic mechanisms like -tocopherol (vitamin E), ascorbic acid (vitamin C), polyphenolics, flavonoids, and carotenes are some examples of these mechanisms (Cheng et al., 2020). Superoxide dismutase, which exists in three different forms in plants (Mn-SOD in the mitochondrial matrix, Fe-SOD in the chloroplasts, and Cu-Zn SOD in the cytosol, chloroplasts, and possibly the extracellular space), dismutates superoxide radicals into H2O2 and can thereby prevent the formation of OH, which is involved in lipid peroxidation (Imlay, 2003). APX, MDHAR, DHAR, and GR are all components of the AsA-GSH cycles, which can be used to eliminate hydrogen peroxide (Bailly, 2004). The regeneration of potent antioxidants like vitamin C, vitamin E, and glutathione (GSH) is also aided by the enzymes of As A-GSH (Fig. 1). Lipid peroxidation produces lipid peroxyl radicals (LOO), which are lipid-free radicals that can be neutralized by vitamin E to produce the corresponding nonradical lipid product and -tocopherol radicals. Scavengers like vitamin C can efficiently resist ROS. In the meantime, the antioxidant form of vitamin E can be renewed by reducing -tocopherol radicals. The excessive production of ROS and an impaired antioxidant system during seed deterioration will cause some physiological imbalances in the seed, which will ultimately cause a loss of viability and germinability (Oenel et al., 2017). These physiological imbalances will result in lipid peroxidation, protein carbonylation, and genetic damage. According to research, most genes involved in oxidative stress were down-regulated when Pisum sativum seeds were artificially aged for 15 days at 50 C and 60% RH (Chen et al., 2013). Similar results were also observed in seeds of Zea mays (Su et al., 2018).

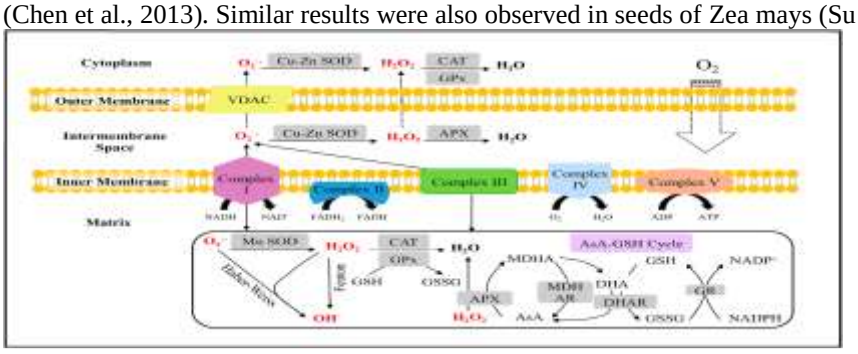

Figure 5. Major reactions that generate and eliminate reactive oxygen species (ROS) during seed deterioration. APX, ascorbate peroxidase; AsA, ascorbic acid; CAT, catalase; DHA, dehydroascorbate; DHAR, dehydroascorbate reductase; GPx, glutathione peroxidase; GR, glutathione reductase; GSH, reduced glutathione; GSSG, oxidized glutathione; MDHA, monodehydroascorbate; MDHAR, mono dihydro ascorbate reductase; NADP+, nicotinamide adenine dinucleotide phosphate; NADPH, reduced form of NADP+; SOD, superoxide dismutase.

Source (Zhang et al. (2021)

Lipid peroxidation

The disintegration of the plasma membrane, predominantly brought on by lipid peroxidation, is one significant process that occurs when seeds deteriorate (Ebone et al., 2019). Increased levels of ROS attack polyunsaturated fatty acids in membrane phospholipids as seeds deteriorate, changing membrane permeability and causing membrane destruction by breaking down long-chain fatty acids into smaller compounds (Oenel et al., 2017).

Lipid peroxidation is an automatic process that, once it begins, self-replicates and accelerates (Fig. 5). The general mechanism has traditionally been broken down into three steps: reaction one initiates the process, reactions 2-4 propagate it, and reactions 5 and 6 terminate it (Apel & Hirt, 2004). Aldehydes, ketones, alkanes, carboxylic acids, and polymerization products are a few examples of the generally stable, lipid-soluble chemicals that are the end products of lipid peroxidation (Min et al., 2017). These substances can easily pass through cellular membranes after diffusing from the point of production (Oenel et al., 2017). Additionally, these products are frequently highly reactive and impact the cell's extracellular matrix and other cellular elements (Bhattacharjee, 2019).

Malondialdehyde (MDA), one of the reactive aldehydes, is frequently utilized as a sign of lipid peroxidation. Protein oxidation, which can be mediated by the MDA and result in protein fragmentation, modification, aggregation, and conformational changes, will eventually impact how proteins function (Ebone et al., 2019).ultimately result in modifications to how proteins operate (Ebone et al., 2019).

The MDA concentrations increased 57.5% and 64.23%, respectively, when compared to controls when seeds of Glycine max were accelerated aged at 42 C, 99% RH for three and seven days; this showed lipid peroxidation had resulted in membrane damage (Min et al., 2017). On the other hand, lipoxygenase can potentially catalyze lipid peroxidation by using phospholipid membrane components as substrates (Ebone et al., 2019). However, these aldehydes become the most active when the seed moisture level exceeds 14% (Copeland & McDonald, 2012). As a result, lipid peroxidation can occur in different ways under different situations during rapid aging (lipoxygenase) and long-term storage (autoxidation) (Bailly, 2004). Three LOX-related genes that are overexpressed in rice seeds can speed up the breakdown of membrane integrity, whereas reduced LOX-related gene expression can boost seed vigor while the seeds are being stored (Gayen et al., 2015).

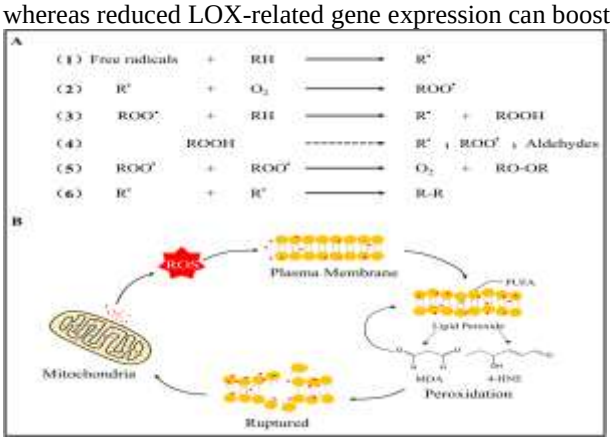

Figure 6. Free radical chain reactions (A) and conceptual model (B) of lipid peroxidation process. The interaction of ROS and other free radicals with polyunsaturated fatty acids (PUFA) in membrane phospholipids (RH) usually initiates the process of lipid peroxidation and results in the formation of lipid radicals (R·) (reaction 1); the R· can react with available O_2 to generate lipid peroxyl radicals (ROO·) (reaction 2) that, in turn, can attack another lipid molecule to generate lipid hydroperoxide (ROOH) (reaction 3) and thereby propagate the chain reaction. The unstable ROOH degrades and breaks down, which leads to the production of other radical species (e.g., RO· and ROO·), which then propagate additional lipid peroxidation; these may also produce several aldehydic end-products, including 4-Hydroxy-2, 3-nonenal (HNE) and malonyl dialdehyde (MDA) (reaction 4); this chain reaction terminates when a ROO· or R· reacts with a similar radical to form nonradical products (adduct) (reactions 5 and 6). As a result, long-chain fatty acids break down into smaller compounds, and the membranes lose their integrity (B).

Source: Zhang et al. (2021)

Protein carbonylation

Proteins can be modified and damaged by elevated ROS levels during seed aging, some of which are irreversible and can cause protein damage, aggregation, and degradation (Moller et al., 2020). Carbonylation is the most well-studied irreversible protein oxidation during seed degeneration (Moller et al., 2020). The level of protein carboxylation increased with treatment time. It significantly correlated with ROS content when non-dormant seeds of Arabidopsis thaliana were held at 40 C and 85% RH (i.e., accelerated aging) (Rajjou et al., 2008). Carbonyl groups can be incorporated into proteins through direct metal-catalyzed oxidation of some amino acids (e.g., arginine, lysine, proline, and threonine residues (Satour et al., 2018) or indirectly by reactions between nucleophilic centers within those amino acids with reactive carbonyl species (RCS) that are derived from lipid peroxidation, such as HNE and MDA (Smakowska et al., 2014).

Protein functions may be slowed down by carbonylation. Carbonylated cellular proteins may undergo proteasome-dependent degradation, or they may organize into similar aggregates, such as combinations of highly carbonylated proteins with high molecular weights that have been unfolded or damaged (Hohn et al., 2013), to prevent the accumulation of those toxic products. This reduces or eliminates the targeted protein catalytic activities (Winger et al., 2007). In plant cells, carbonylated proteins can be detected in some cellular compartments, including the cytosol, peroxisomes, and mitochondria (Li et al., 2017). Complexes I and III of the mitochondrial electron transport system are particularly vulnerable to carbonylation and oxidation than other cellular compartments since mitochondria are the primary organelles that create ROS (Li et al., 2017). HNE-adduction and carbonylation have been used to modify some proteins in ETC (Winger et al., 2007).

After further analysis of protein spots with deeper carbonylation, it was discovered that carbonylated proteins were primarily concentrated in the TCA cycle (malate dehydrogenase), glycolysis (photo glycerate mutase, pyruvate

decarboxylase, triose phosphate isomerase), ATP synthesis (ATP synthase subunit alpha), mitochondrial processing (mitochondrial-processing peptidase subunit alpha), intra This kind of evidence suggests that protein carbonylation will lead to the protein's loss of integrity and function, the inactivation of the TCA cycle, ETC enzymes, and eventually seed death (Chen et al., 2019).

Genetic damage

Additionally, genetic damage can result from increased levels of ROS during seed aging. Genetic deterioration is cited as the main reason for seed aging by Harrington (1972). After a certain amount of chromosomal damage, including DNA strand breaks, DNA methylation, and aberrant gene expression, has been accumulated during seed aging, the ability of the seed to germinate is lost (Harrington, 1972). For instance, all variable seeds from Oryza sativa and Pisum sativum that were aged at 45 °C showed a decrease in the mitotic index and an increase in the frequency of chromosomal damage; in addition, an increase in storage time led to an increase in DNA damage (Dantas et al., 2019). According to Cheah and Osborne (1978), the main cause of chromosome aberrations was the accumulation of DNA lesions, such as base modifications and single or double-strand breaks. According to Sano et al. (2016), ROS, particularly OH, are typically the primary cause of DNA strand breaks by directly inducing desaturation of deoxyribose units or generating covalent changes of bases. One significant alteration that can occur is guanine hydroxylation at the C-8 position, which yields 8-hydroxy-2′-deoxyguanosine (8-OHdG) (Sano et al., 2016).

Additionally, 8-OHdG has the potential to cause mutations because it can mis-pair with either adenine (A) or cytosine (C), causing a transversion of GC to TA during DNA replication (Sano et al., 2016). Germination depends on proper translation and transcription since DNA alterations may disrupt these processes. In this context, this kind of DNA damage may be linked to a loss of viability (Sano et al., 2016). The single-stranded structure of RNA makes it more susceptible to oxidation than DNA, which may cause RNA to break down. According to Fleming et al. (2017), as Glycine max's germinability decreased, so did the incorporation of different radioactive RNA precursors into all the major types of RNA.

Additionally, the processing of RNA precursors into the ribosomal subunits' 18 S and 25 S RNA may have been delayed. Additional research using electrophoresis to study RNA degradation revealed that 23 S and 13 S rRNA, two small and fast kinds of RNA, were generated due to the progressive decay of 25 S and 18 S rRNA. Following hydration, the nonviable S. cereale embryos did not convert radioactive amino acids from an external source into protein.

Breakdown of the repair system

Seeds can minimize damage to biological molecules and cellular structures since they have strong healing mechanisms. The speed and capacity of a seed to repair itself are closely related to performance during germination and the establishment of young seedlings. Once seed imbibition occurs, the repair of cellular structures can facilitate the ability of seeds to recover from damage that occurs during dormancy prior to the beginning of germination (Long et al., 2015). However, the molecular mechanisms of RNA repair have yet to be fully understood, as they have not received as much attention in earlier studies on seed aging as DNA and protein repair have (Sano et al., 2016). Base excision repair (BER) is a method for repairing DNA base damage or single-stranded DNA breaks (Sano et al., 2016). The DNA glycosylase enzymes that repair various cell products typically start the BER pathway by creating abasic or apurinic/apyrimidinic (AP) sites. After the damaged site is removed, DNA synthesis takes place to fill the gap in the DNA sequence. AtOGG1, a DNA glycosylase/apurinic/apyrimidinic (AP) lyase found in Arabidopsis, takes part in base excision repair, eliminating 8-oxo-dG from DNA. Increased seed resilience to accelerated aging will result from overexpression of this gene, and the 8-oxoG content of transgenic seeds will decline, which indicates its involvement in the repair of damage to DNA and the high level of germination ability of the seeds during abiotic stress (Chen et al., 2012). Due to the extreme cytotoxicity of double-strand breaks, DNA damage is either directly produced by ROS or indirectly generated by the BER process in products. Based on the activity of DNA ligases, the DSBs are repaired by homologous recombination (HR) or non-homologous end joining (NHEJ). According to a Waterworthet al. (2010) study, an Arabidopsis mutant with a DNA ligase IV deficiency exhibited notable responsiveness to controlled seed aging.

The nonenzymatic conversion of L-aspartyl residues into L-iso aspartyl residues is one instance of how protein can be harmed during dry storage. However, this harm can be repaired by the protein L-iso aspartyl methyltransferase (PIMT), particularly during seed growth and imbibition (Mudgett et al., 1997). Although seeds contain a variety of repair mechanisms to deal with ROS damage, damage eventually builds up in DNA, RNA, and proteins necessary for seed germination after a protracted period of storage or accelerated aging therapy. Seeds that have sustained irreparable damage will no longer be viable and will not germinate (Xu et al., 2020).

Programmed cell death

Plants use programmed cell death as a controlled strategy for cell suicide in response to internal and external stimuli (Biswas et al., 2020). The initial focus of PCD research was on animal cells. However, it has since been noted that PCD is also involved in some plant life processes, including pollen tube burst during fertilization, lateral and adventitious root emergence, and seed development and germination (Van Hautegemet al., 2015). According to Hu et al. (2012) (Fig. 6), PCD events may also be related to the loss of seed viability that occurs with seed aging. By facilitating the opening of mitochondrial membrane permeability transition pores (MPTPs), which in turn causes the release of Cyt C from inter-membrane spaces of mitochondria into the cytoplasm, excessive ROS production from mitochondria during seed aging may induce PCD (Wang et al., 2015). High Cyt C levels in the cytoplasm have been found to start the caspase and downstream proteolytic cascade in animal cells, which is thought to be the main execution switch for PCD. The nucleus will be invaded

by activated caspase-like enzymes, which will cause the characteristic nuclear alterations associated with PCD, including DNA breakage, chromatin condensation, and nucleus disruption (Nigam et al., 2019). Damaged seeds of Triticum aestivum (Li et al., 2018), Pisum sativum (Kranner et al., 2011), Secale cereal, and Ulmuspumila (Hu et al., 2012) have been shown to contain a DNA ladder. It is crucial that although DNA laddering can show that a certain pattern of DNA fragmentation exists, it can be challenging to show this pattern electrophoretically in extracts when only some of the cells are fragmenting (Song et al., 2007). As a result, not all species, such as Glycine max, participate in DNA laddering during seed deterioration (Song et al., 2007). It is possible to study PCD in individuals using in situ observations, such as the terminal deoxynucleotidyl transferase (TdT)-mediated dUTP nick end labeling (TUNEL) assay. TUNEL-positive nuclei increased with accelerated aging time, indicating that DNA fragmentation had taken place. Due to this, it may be possible to detect DNA fragmentation using a combination of the TUNEL assay and isolated DNA electrophoresis (Song et al., 2007).

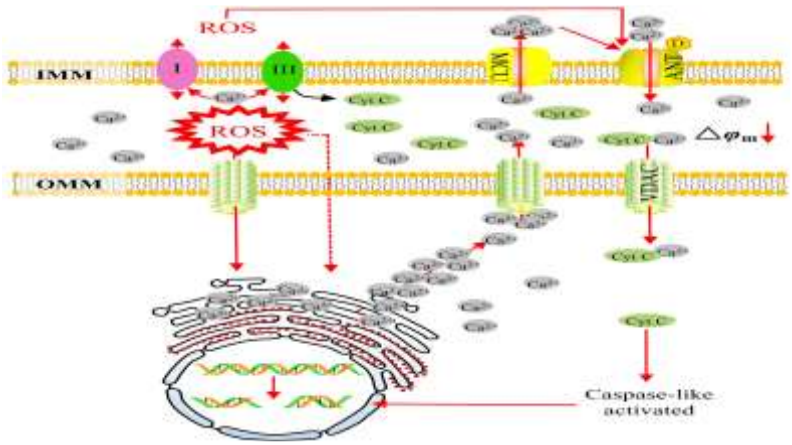

Figure 7. Schematic representation of ROS-dependent signaling involved in programmed cell death. Increased reactive oxygen species (ROS) production from mitochondria may trigger Ca2+ influx from the endoplasmic reticulum (ER), and cytoplasm enters the mitochondrial matrix through voltage-dependent anion channels (VDAC) or calcium uniporter (MCU). High levels of Ca2+ in the mitochondrial stimulate respiratory chain (I and III) activity, leading to higher amounts of ROS, which can further lead to the increased release of Ca2+. Further, the increased ROS and Ca2+ load in mitochondria will promote the opening of mitochondrial permeability transition pores (MPTPs); which span the inner (IMM) and outer mitochondrial membranes (OMM) and are mainly composed of cyclophilin D (D) adenine nucleotide translocator (ANT), and VDAC; the prolonged opening of MPTP leads to a significant increase in the permeability of the IMM to solutes with molecular masses <1500 Da, as a consequence of the charge difference between the mitochondrial matrix and the cytosol (mitochondrial membrane potential, ΔΨm). Subsequently, mitochondria swell irreversibly, causing rupturing the OMM while releasing cytochrome C (Cyt C) from inter-membrane space to the cytoplasm; high Cyt C levels will initiate the activity of caspase-like enzymes, which will enter the nucleus, resulting in typical PCD changes such as DNA fragmentation and disruption of the nucleus.

Source: Zhang et al. (2021)

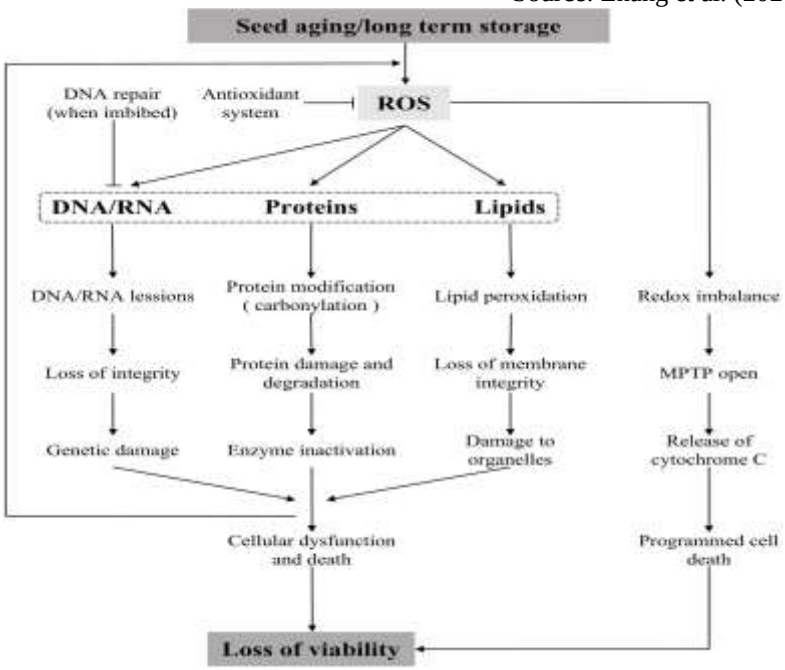

Figure 8. Conceptual model of the role of reactive oxygen species (ROS) during seed aging. MPTP, mitochondrial permeability transition pore.

Source: Zhang et al. (2021)

Discussions of Practical Approaches to Overcome Seed Deterioration, Improve Seed Performance and Its Longevity

Some practical and effective approaches can help different kinds of seeds to withstand deterioration.

Seed priming

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). Primed seeds usually have higher and synchronized germination (Farooq et al., 2009) owing to simply a reduction in the lag time of imbibition taking place (Brock-lehurstand, 2008), build-up of germination-enhancing metabolites (Farooq et al., 2006), metabolic repair during imbibition (Bray et al., 1989) and osmotic adjustment (Bradford, 1986). Priming of seeds has been reported to reverse some of the aging-induced deteriorative events and thus improve seed performance (Taylor et al., 1998) 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). Many seed priming treatments have been used to reduce the damage of aging and invigorate their performance in many crops (Farooq et al., 2009). Priming appears to reverse the detrimental effects of seed deterioration by increasing the activities of free radical scavenging enzymes such as catalase, peroxidase, and glyoxysomal enzymes such as isocitrate lyase and malate synthase as well as by counteracting the effects of lipid peroxidation. Activation of DNA replication and enhancement of RNA and protein synthesis following priming has also been reported. Furthermore, the ATP levels have been found to increase during priming.

Addition of plant growth regulators

The exogenous application of plant growth regulators like GA_3, Kinetin, ABA, and Indole-3-butyric acid prior to storage has been found to retard seed deterioration and maintain seed vigor and germination.

CONCLUSIONS

Seed deterioration is the loss of seed quality (vigor and viability), resulting in poor seed germination and seedling establishment. A crucial part of seed quality during crop production is seed vitality, a key quality characteristic of seeds. Even under ideal storage circumstances, all seeds will eventually lose viability, which causes a significant loss for species that are vital commercially. It is known that various unique but interrelated variables affect seed viability. These include the environment for storage, particularly in terms of temperature and relative humidity, as well as the genetic, maturational, and harvest factors. There are several sources of loss in seed quality during pre-harvest (field weathering), harvest (handling), and post-harvest (storage) periods. The deterioration lowers the seed morphological structure, causing damage to genetic material, physiological quality, ultra-structural damage, and biochemical activity such as loss of seed protection capacity, lipid peroxidation, and consumption of reserves, ultimately accelerating the deterioration process. Many factors can contribute to seed deterioration; however, oxidation damage caused by free radicals and ROS is the main reason. By breaking down lipids and releasing by-products, such as reactive aldehydes that can harm proteins and nucleic acids, ROS can trigger the peroxidation of lipids by reacting with polyunsaturated fatty acids in membrane phospholipids. They can significantly change and impact protein activity when interacting with it, leading to functional inactivation and metabolic malfunction of the protein. Through their interactions with DNA, ROS have the potential to cause strand breakage and the production of adducts, including 8-hydroxy-deoxy-guanidine (8-OHdG). These actions might be connected and paint a broad picture of how cellular organization has broken down. However, many concerns about how ROS affects seed aging need to be studied. For instance, new research has indicated that ROS may cause PCD by causing a change in the permeability of the mitochondrial membrane and releasing Cyt C. However, no PCD and ROS sensing signal transduction genes have yet been identified. Furthermore, it is yet to be discovered how to control the synthesis and activity of redox buffers or antioxidants, given the interactions and crosstalk between ROS and other signaling systems. Several controlled seed hydration techniques (seed priming) and exogenous application of plant growth regulators can be applied to improve seeds' seed quality (viability and vigor) and germination potential.

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