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Jayesh B Kadavala
Research Scholar, Department of Seed Science and Technology, B.A. College of Agriculture, Anand Agricultural University, Anand, Gujarat, India

Dr. MB Patel
Associate Research Scientist & AMP, Unit Head Main Maize Research Station, Anand Agricultural University, Anand, Godhra, Gujarat, India

Dr. PK Parmar
Assistant Research Scientist, Main Maize Research Station, Anand Agricultural University, Anand, Godhra, Gujarat, India

Dr. Kalyanrao Patil
Assistant Professor and Head, Department of Seed Science and Technology, Anand Agricultural University, Anand, Gujarat, India

Corresponding Author:
Jayesh B Kadavala
Research Scholar, Department of Seed Science and Technology, B.A. College of Agriculture, Anand Agricultural University, Anand, Gujarat, India

Seed ageing physiological, biochemical and molecular basis: A review

Jayesh B Kadavala, Dr. MB Patel, Dr. PK Parmar and Dr. Kalyanrao Patil

Abstract
Seed ageing is a natural process that causes the decline in seed viability and vigor over time, leading to reduced germination and seedling establishment. This phenomenon is of great concern to plant breeders and seed producers, as it affects seed quality and consequently, crop yield. The physiological, biochemical, and molecular mechanisms underlying seed ageing have been extensively studied in recent years. Physiologically, ageing seeds undergo a series of complex biochemical changes, including lipid peroxidation, protein oxidation, DNA damage, and changes in the antioxidant system. These changes result in reduced energy metabolism, decreased membrane integrity, and impaired germination potential. At the molecular level, ageing seeds experience alterations in gene expression, DNA methylation, and chromatin modification, affecting the regulation of stress response and development pathways. To better understand the underlying mechanisms of seed ageing, numerous studies have employed omics technologies such as genomics, transcriptomics, proteomics, and metabolomics. This review provides an overview of the physiological, biochemical, and molecular basis of seed ageing, with a focus on recent advances in the field. Understanding the mechanisms of seed ageing can help develop strategies to improve seed quality and increase crop productivity.

Keywords: Seed ageing, seed deterioration, physiological, biochemical, molecular, reactive oxygen species (ROS), seed viability

1. Introduction

Seed ageing refers to the natural process of deterioration that occurs in seeds over time, resulting in a decrease in their viability and vigor. This phenomenon has been the subject of extensive research over the years, as it has significant implications for agriculture and the preservation of plant genetic resources. Understanding the physiological, biochemical, and molecular basis of seed ageing is crucial for developing effective strategies to prolong seed longevity and ensure the preservation of valuable germplasm.

Physiologically, seed ageing is characterized by a gradual decline in seed quality, which manifests as a reduction in germination rates, seedling vigor, and overall plant performance. This decline is caused by a variety of factors, including the accumulation of reactive oxygen species (ROS), changes in membrane lipid composition and fluidity, and alterations in gene expression and protein synthesis.

Biochemically, seed ageing is associated with changes in the levels and activities of various enzymes and metabolic pathways, which can affect seed viability and germination. Germination is the first step in growth and development of crops (Mohsen-Nasab *et al*. 2010) [34]. Germination rate, germination uniformity and seed vigour are important parameters in seed quality and thus affect plant status. During germination, with increasing moisture content of seeds, production of reactive oxygen species (ROS) occurs through two processes: biochemical reactions in mitochondria or glyoxysome, and release of ROS from substances that are produced in different seed tissues during harvest and stored in dry seeds (Zamani *et al*. 2010) [35]. During seed sotrage, ROS such as superoxide radicals (O2-), hydrogen peroxide (H_2O_2) and hydroxyl radicals (OH•), accumulate in ageing seed tissues and have a vital role in seed vigour reduction (Pukacka, Ratajczak 2005) [36]. Accumulation of ROS leads to their reaction with unsaturated fatty acids and causes changes in cell membranes, such as lipid peroxidation and ultimately its destruction.

The ability of seeds to produce antioxidative enzymes considerably differs depending on species and genotype. Enzymatic detoxification and repair of cell membranes are the main means to delay ageing (Tavakol Afshari *et al*. 2007) [37]. ROS scavenging enzymatic systems, such as superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD) and non-enzymatic antioxidants such as β-carotene, ascorbic acid, α-tocopherol, reduced glutathione can counteract the harmful effects of ROS in plant tissues (Kibinza *et al*. 2006) [38]. Activity of these metabolites and antioxidant enzymes causes high levels of seed resistance to oxidative damage and minimizes damage to cells (Tabatabaei 2015) [39].

Molecularly, seed ageing is linked to changes in gene expression and epigenetic modifications, which can affect a wide range of cellular processes. Studies have shown that ageing seeds exhibit alterations in the expression of genes involved in stress responses, DNA repair, and cell signaling, among others. Additionally, epigenetic modifications such as DNA methylation and histone acetylation have been shown to play a role in seed ageing, potentially influencing gene expression and chromatin structure.

The study of seed ageing has important implications for agriculture and the preservation of plant genetic resources. In agriculture, the loss of seed viability over time can result in reduced crop yields and lower seedling establishment rates, leading to economic losses for farmers. Additionally, the preservation of plant genetic resources is critical for maintaining biodiversity and ensuring the long-term sustainability of agriculture. Understanding the physiological, biochemical, and molecular basis of seed ageing is therefore essential for developing effective strategies for seed storage and preservation.

2. Physiological changes during seed ageing

2.1 Loss of membrane integrity

Loss of membrane integrity is a common physiological change that occurs during seed aging. Membranes play a crucial role in maintaining the structural and functional integrity of cells, and any damage or disruption to the membrane can affect cellular processes and reduce seed viability. During seed aging, the integrity of the cell membrane can be compromised due to the production of reactive oxygen species (ROS) and oxidative damage. ROS can cause lipid peroxidation, which can lead to the degradation of membrane lipids and a loss of membrane integrity (Bailly *et al*., 2008) [12]. As a result, electrolytes and other cellular components can leak out of the cell, leading to a decline in seed viability. In addition to oxidative damage, other factors can also contribute to the loss of membrane integrity during seed aging. For example, temperature and moisture can affect the fluidity and stability of membranes, leading to membrane damage and reduced seed viability (Kumar and Sharma, 2018) [21].

2.2 Decrease in protein content

Seed aging is often associated with a decline in protein content, which can affect seed germination and vigor. The decrease in protein content is due to the breakdown of proteins and other metabolic changes that occur during seed aging. Proteins play a critical role in seed development, and they are essential for various metabolic and cellular processes. For example, proteins are involved in the synthesis of enzymes, hormones, and structural components, as well as the regulation of gene expression and signal transduction pathways.

During seed aging, proteins can become degraded due to various factors, including the production of reactive oxygen species (ROS) and other oxidative damage. ROS can cause protein oxidation and fragmentation, leading to a decline in protein content and quality (Bailly *et al*., 2008) [12]. Other factors, such as temperature, moisture, and storage conditions, can also contribute to protein degradation and reduce seed quality (Huang *et al*., 2018) [3]. The decrease in protein content can affect seed germination and vigor by reducing the availability of essential nutrients and enzymes required for growth and development. In addition, proteins can also act as protective agents against stress, and their decline can make the seed more vulnerable to environmental stress and other factors that can reduce seed viability.

2.3 Accumulation of free radicals

During seed aging, one of the physiological changes that occur is the accumulation of free radicals. Free radicals are highly reactive molecules that contain unpaired electrons and can cause damage to cellular components, including DNA, lipids, and proteins. The accumulation of free radicals is due to the imbalance between the production and removal of reactive oxygen species (ROS). ROS are produced during normal metabolic processes, such as respiration and photosynthesis, and they play a crucial role in various physiological processes, such as signaling and defense against pathogens. However, under stressful conditions, the production of ROS can increase, leading to oxidative stress and the accumulation of free radicals. In seeds, aging is one of the major factors that can increase ROS production and lead to the accumulation of free radicals. The accumulation of free radicals can have several deleterious effects on seed quality and viability. For example, free radicals can cause lipid peroxidation, leading to the degradation of membrane lipids and loss of membrane integrity, which can result in decreased seed viability. Free radicals can also cause protein oxidation and fragmentation, leading to a decline in protein content and quality, which can affect seed germination and vigor (Bailly *et al*., 2008) [12].

2.4 Alterations in gene expression

Seed aging can also lead to alterations in gene expression, which can affect various physiological processes, such as metabolism, growth, and development. The changes in gene expression are due to various factors, including oxidative stress, DNA damage, and epigenetic modifications. Oxidative stress and DNA damage can lead to alterations in gene expression by affecting the stability and function of DNA, as well as by activating various signaling pathways that regulate gene expression. For example, oxidative stress can lead to the activation of stress-responsive genes, such as those encoding antioxidant enzymes and heat shock proteins, which can help protect the cell from further damage (Duan *et al*., 2017) [4]. Epigenetic modifications, such as DNA methylation and histone modifications, can also affect gene expression and contribute to seed aging. DNA methylation, for example, can regulate gene expression by affecting the accessibility of DNA to transcription factors, while histone modifications can affect the structure and function of chromatin, which can affect gene expression and cellular processes (Hatzig *et al*., 2015) [5].

The alterations in gene expression can affect seed germination and vigor by affecting various physiological processes. For example, changes in gene expression can affect the availability of essential nutrients and enzymes required for growth and development, as well as the response to environmental stress and other factors that can affect seed viability.

2.5 Loss of mitochondrial function

Mitochondria are organelles that play a vital role in cellular respiration, energy production, and metabolism. They are also involved in various cellular processes, such as apoptosis, calcium signaling, and reactive oxygen species (ROS) production. During seed aging, loss of mitochondrial function is a common physiological change that occurs. The loss of mitochondrial function is due to various factors, including oxidative stress, protein damage, and mitochondrial DNA (mtDNA) mutations. Oxidative stress can cause damage to mitochondrial membranes and enzymes, leading to decreased mitochondrial respiration and ATP production. Protein damage, such as oxidation and fragmentation, can also affect mitochondrial function by disrupting the structure and function of mitochondrial enzymes and transporters (El-Maarouf-Bouteau *et al*., 2011) [7].

Furthermore, mtDNA mutations can accumulate over time and affect mitochondrial function. mtDNA mutations can affect the expression of mitochondrial genes and proteins, leading to decreased mitochondrial respiration and ATP production. mtDNA mutations can also affect mitochondrial biogenesis, fusion, and fission, leading to alterations in mitochondrial morphology and function (Birky *et al*., 2013) [6]. The loss of mitochondrial function can have several deleterious effects on seed quality and viability. For example, the decrease in ATP production can affect various physiological processes, such as metabolism and growth, and can lead to decreased seed viability. Furthermore, the accumulation of ROS in mitochondria can cause oxidative damage to cellular components, such as lipids, proteins, and DNA, leading to further loss of seed viability (Foyer and Noctor, 2011) [8].

To prevent the loss of mitochondrial function and maintain seed quality during storage, it is important to store seeds under appropriate conditions. This may include using low-temperature storage to slow down metabolic processes and reduce oxidative damage, as well as using mitochondrial-targeted antioxidants to reduce the production of ROS and maintain mitochondrial function.

2.6 Inability of ribosomes to dissociate

Ribosomes are cellular organelles responsible for protein synthesis. During seed aging, the inability of ribosomes to dissociate is a common physiological change that occurs. This is due to various factors, including oxidative damage to ribosomal proteins and RNA, as well as changes in ribosomal protein composition. Oxidative damage can cause fragmentation and cross-linking of ribosomal proteins and RNA, leading to decreased ribosomal activity and stability. Furthermore, the accumulation of ROS can lead to the formation of carbonyl groups on ribosomal proteins, which can affect the structure and function of the ribosome (Liu *et al*., 2013) [10].

Changes in ribosomal protein composition can also affect the dissociation of ribosomes. During seed aging, there is a decrease in the expression of some ribosomal protein genes, which can lead to altered ribosomal protein composition and decreased ribosomal activity (Ding *et al*., 2019) [9]. The inability of ribosomes to dissociate can have several deleterious effects on seed quality and viability. For example, it can lead to the accumulation of abnormal proteins and aggregates, which can interfere with cellular processes and lead to decreased seed viability. Furthermore, it can lead to a decrease in protein synthesis, which can affect various physiological processes, such as metabolism and growth, and can lead to decreased seed viability.

2.7 Starvation of meristemetic Cell

The meristematic cells are responsible for the growth and development of plants. During seed aging, one of the physiological changes that occur is the starvation of meristematic cells. This is due to various factors, including oxidative stress, decreased nutrient availability, and altered hormonal regulation. Oxidative stress can cause damage to cellular membranes, proteins, and DNA, leading to decreased cellular function and viability. The decrease in nutrient availability, such as carbohydrates and amino acids, can also affect meristematic cell function by limiting energy production and cellular metabolism. Furthermore, alterations in hormonal regulation, such as changes in the ratio of auxin to cytokinin, can lead to altered cell division and differentiation, affecting meristematic cell activity (El-Maarouf-Bouteau *et al*., 2013) [11].

The starvation of meristematic cells can have several deleterious effects on seed quality and viability. For example, it can lead to a decrease in plant growth and development, affecting seedling emergence and vigor. Furthermore, it can lead to the accumulation of abnormal cells and tissues, affecting the overall quality of the plant. To prevent the starvation of meristematic cells and maintain seed quality during storage, it is important to store seeds under appropriate conditions. This may include using low-temperature storage to slow down metabolic processes and reduce oxidative damage, as well as using appropriate seed treatments, such as priming or coating, to improve seed vigor and germination.

2.8 changes in the antioxidant system

During seed aging, there are changes in the antioxidant system, which is responsible for protecting cells from oxidative stress caused by reactive oxygen species (ROS). ROS are generated during normal cellular processes, but their levels can increase during seed aging, leading to oxidative damage to biomolecules, including lipids, proteins, and DNA. The antioxidant system includes enzymes such as superoxide dismutase (SOD), catalase (CAT), and peroxidases (POX), as well as non-enzymatic antioxidants such as ascorbic acid, α-tocopherol, and glutathione. These antioxidants work together to scavenge ROS and prevent oxidative damage (Gao *et al*. 2015) [26].

Studies have shown that during seed aging, the activity of antioxidant enzymes can decline, leading to an accumulation of ROS and oxidative damage to biomolecules. For example, the activity of SOD, which converts superoxide radicals to hydrogen peroxide, has been found to decrease in aged seeds of various species. The activity of CAT, which converts hydrogen peroxide to water and oxygen, has also been shown to decline during seed aging in some species (Kibinza *et al*. 2006) [38].

In addition to changes in enzyme activity, there can be alterations in the levels of non-enzymatic antioxidants during seed aging. For example, the levels of ascorbic acid and α-tocopherol have been found to decrease in aged seeds of some species, which can lead to increased oxidative damage. To maintain seed quality during aging, it is important to maintain a balance between ROS production and the antioxidant defense system. Strategies to enhance the antioxidant system in aged seeds include the application of exogenous antioxidants, such as ascorbic acid and α-tocopherol, and the use of priming treatments, which involve soaking seeds in a solution that enhances antioxidant activity (Kranner and Colville, 2011) [25].

Overall, changes in the antioxidant system during seed aging can have significant impacts on seed viability. Understanding these changes can help identify strategies to enhance the antioxidant defense system and maintain seed quality during storage.

3. Biochemical changes during seed ageing

3.1 Lipid peroxidation

Lipid peroxidation is a process that occurs when free radicals attack the unsaturated fatty acids in cell membranes, resulting in the oxidation and degradation of these lipids. This process can cause damage to the cell membrane, leading to decreased membrane integrity and increased permeability. Lipid peroxidation is one of the major biochemical changes that occur during seed aging, as it leads to membrane leakage and loss of integrity, affecting seed viability (Bailly *et al*. 2008) [12]. The process of lipid peroxidation can be triggered by various factors, including high temperatures, oxidative stress, and exposure to UV radiation. It is also influenced by the fatty acid composition of the membrane, with unsaturated fatty acids being more susceptible to peroxidation than saturated fatty acids. The products of lipid peroxidation can also have toxic effects on cells, as they can react with other cellular components, such as proteins and DNA, leading to further damage. Antioxidant systems within cells can help to prevent lipid peroxidation by neutralizing free radicals and other reactive oxygen species (Moller *et al*. 2007) [13].

3.2 Protein oxidation

Protein oxidation is a process that occurs when reactive oxygen species (ROS) attack and modify the amino acid residues of proteins, resulting in the degradation of the protein's structure and function. This process can lead to the formation of protein carbonyls, which are markers of oxidative damage, and can accumulate during seed aging (Bailly *et al* 2008) [12].

Protein oxidation is one of the major biochemical changes that occur during seed aging, leading to decreased seed quality and viability. Proteins play a critical role in seed germination and growth, and oxidative damage to proteins can affect their structure and function. Protein oxidation during seed aging can lead to a decrease in enzyme activity, an increase in protein aggregation, and a decrease in protein solubility. (Moller *et al*. 2007) [13].

3.3 Changes in sugar metabolism

Changes in sugar metabolism are among the biochemical changes that occur during seed aging. The levels of sugars, such as glucose, fructose, sucrose, and raffinose, can change during seed aging. The metabolism of sugars plays a critical role in seed germination and growth, as they provide the energy and carbon skeletons needed for the development of the embryo and the establishment of the seedling. During seed aging, the balance between sugar synthesis and degradation can be disrupted, leading to changes in sugar metabolism (Bailly *et al*. 2008) [12].

Studies have shown that the levels of soluble sugars, such as glucose and fructose, decrease during seed aging, while the levels of oligosaccharides, such as raffinose and stachyose, increase. This change in sugar metabolism is thought to be a result of increased activity of enzymes involved in the breakdown of sugars, such as α-amylase and β-glucosidase, and a decrease in the activity of enzymes involved in the synthesis of sugars, such as sucrose synthase (Farrant *et al*. 2011) [16].

The changes in sugar metabolism during seed aging can affect seed germination and vigor. For example, a decrease in the levels of soluble sugars can limit the availability of energy and carbon skeletons for the developing embryo and seedling, while an increase in the levels of oligosaccharides can affect seed germination by reducing water uptake and increasing the osmotic potential of the seed.

3.4 Changes in reactive oxygen species (ROS) levels

Reactive oxygen species (ROS) are highly reactive molecules that can cause oxidative damage to biological macromolecules, such as lipids, proteins, and nucleic acids. ROS levels can increase during seed aging due to various factors, such as the breakdown of cellular components, imbalances in redox homeostasis, and the accumulation of damaged mitochondria (Bailly *et al*. 2008) [12].

The accumulation of ROS during seed aging can cause oxidative damage to the cell membrane and other cellular components, leading to the loss of seed viability and vigor. Studies have shown that the levels of ROS, such as hydrogen peroxide (H2O2), superoxide anion (O2−), and hydroxyl radicals (OH−), increase during seed aging (Iqbal and Nazar 2014) [15].

3.5 Changes in hormone levels

Changes in hormone levels are among the physiological and biochemical changes that occur during seed aging. Hormones play a critical role in seed development, germination, and growth, and changes in their levels during seed aging can affect seed quality and vigor. Studies have shown that the levels of various hormones, such as abscisic acid (ABA), gibberellins (GA), and cytokinins, can change during seed aging. The levels of ABA, which is a stress hormone that plays a role in seed dormancy and germination, are known to increase during seed aging. This increase in ABA levels can lead to the maintenance of seed dormancy, which can delay or prevent seed germination (Farrant and Moore, J. P. 2011) [16].

On the other hand, the levels of GA, which is a hormone that promotes seed germination and growth, are known to decrease during seed aging. This decrease in GA levels can contribute to the loss of seed vigor and poor germination. Changes in the levels of cytokinins, which are hormones that play a role in cell division and differentiation, have also been observed during seed aging. Studies have shown that the levels of cytokinins can decrease during seed aging, which can affect seed germination and growth (Goggin *et al*. 2015) [17].

To maintain seed quality and viability during storage, it is important to store seeds under appropriate conditions. This may include using low-temperature storage to slow down metabolic processes and reduce oxidative damage, as well as using appropriate seed treatments, such as priming or coating, to improve seed vigor and germination.

4. Molecular changes during seed ageing

4.1 DNA damage

DNA damage can occur during seed aging due to various factors such as oxidative stress, radiation, and exposure to toxins. Oxidative stress is a major contributor to DNA damage in seeds during aging, where reactive oxygen species (ROS) accumulate in the cells leading to oxidative damage to DNA. DNA damage can result in mutations, deletions, or alterations in the DNA sequence, which can affect the overall viability and germination potential of the seed (Cummins *et al*. 1999) [18].

Studies have shown that aging-induced DNA damage can lead to changes in gene expression, ultimately affecting the metabolism of the seed. In addition, DNA damage can activate DNA repair mechanisms, which may consume resources necessary for other essential cellular processes, leading to a decrease in seed vigor and viability (Debnath and Mandal, 2019) [19].

4.2 Changes in gene expression

Changes in gene expression can occur during seed aging, resulting in altered metabolism and reduced seed viability. Studies have shown that aging-induced changes in gene expression can be related to changes in DNA methylation, histone modifications, and small RNA-mediated gene regulation. DNA methylation, which involves the addition of a methyl group to DNA, can affect gene expression by silencing or activating gene expression. Aging-induced changes in DNA methylation have been reported in several plant species, including Arabidopsis, maize, and soybean. These changes in DNA methylation can result in altered gene expression patterns, leading to changes in seed metabolism and reduced seed viability (Debnath and Mandal, 2019) [19]

Histone modifications, such as acetylation, methylation, and phosphorylation, can also affect gene expression by regulating chromatin structure and accessibility to transcription factors. Aging-induced changes in histone modifications have been reported in maize and soybean seeds, which may affect gene expression and ultimately seed viability (Kumar *et al*. 2018) [2].

Small RNAs, such as microRNAs and siRNAs, can regulate gene expression by post-transcriptional gene silencing. Aging-induced changes in small RNA-mediated gene regulation have been reported in Arabidopsis, which may affect gene expression and seed viability (Guan *et al.* 2014) [20].

4.3 Alterations in protein structure and function

During seed aging, alterations in protein structure and function can occur, leading to a reduction in seed viability. Several factors, including free radicals, reactive oxygen species (ROS), and changes in pH and temperature, can cause protein denaturation and aggregation, which can affect protein function. Free radicals and ROS can cause oxidative damage to proteins, leading to changes in protein structure and function. These reactive species can attack amino acid residues in proteins, causing oxidation, cross-linking, and fragmentation, which can alter protein conformation and activity. Studies have shown that antioxidants, such as ascorbic acid and α-tocopherol, can help protect proteins from oxidative damage and maintain protein stability during seed aging (Barba-Espin *et al*. 2011) [22].

Changes in pH and temperature can also affect protein structure and function. Alterations in pH can lead to changes in protein charge, which can affect protein stability and solubility. Changes in temperature can cause protein denaturation and aggregation, leading to loss of protein function. It is important to store seeds at appropriate temperatures and pH levels to minimize the effects of aging on protein stability and function (Finch-Savage and Leubner-Metzger, 2006) [23].

In addition to these factors, changes in gene expression and post-translational modifications, such as glycosylation and phosphorylation, can also affect protein structure and function during seed aging. These changes can lead to altered protein conformation and activity, affecting seed viability (Kibinza *et al*. 2006) [38]. Overall, alterations in protein structure and function can have a significant impact on seed viability during aging. Understanding the mechanisms involved in these changes can help identify strategies to prevent or mitigate the effects of aging on seed proteins and maintain seed quality (Kranner and Colville, 2011) [25].

4.4 DNA methylation

DNA methylation is a type of epigenetic modification that involves the addition of a methyl group to the cytosine base of DNA. This modification is typically associated with gene silencing and can have long-lasting effects on gene expression (Chen *et al*. 2017) [28]. During seed aging, DNA methylation patterns can be altered, leading to changes in gene expression that can impact seed viability and vigor. Studies have shown that DNA methylation can increase during seed aging, leading to a decrease in gene expression and reduced seed viability (Gao *et al*. 2016) [29].

For example, in aged rice seeds, DNA methylation was found to increase in the promoter region of a gene involved in starch metabolism, leading to decreased expression of the gene and reduced seed vigor. Similarly, in aged tomato seeds, DNA methylation was found to increase in the promoter region of a gene involved in cell cycle regulation, leading to decreased expression of the gene and reduced seed germination (He *et al*. 2018) [30]. Interestingly, DNA methylation can also be affected by environmental factors, such as temperature and moisture, which can impact seed aging. For example, exposure of Arabidopsis seeds to high temperature and high humidity during storage was found to increase DNA methylation and decrease seed germination (Li *et al*. 2018) [31].

Overall, DNA methylation is an important epigenetic modification that can impact seed aging and seed quality. Understanding the changes in DNA methylation patterns during seed aging can help identify strategies to maintain seed viability and vigor during storage.

4.5 chromatin modification

Chromatin modification is a process that involves changing the structure of chromatin, the complex of DNA and proteins that make up chromosomes, without changing the DNA sequence. Chromatin modification can have a significant impact on gene expression, and therefore can play a role in seed aging. During seed aging, chromatin modifications can occur that alter the accessibility of DNA to transcription factors, ultimately leading to changes in gene expression. For example, changes in histone modifications, such as acetylation, methylation, and phosphorylation, can impact the structure of chromatin and alter the accessibility of genes to transcription factors (Nguyen *et al*. 2015) [33].

Studies have shown that histone modifications can change during seed aging, leading to altered gene expression and reduced seed viability. For example, in aged soybean seeds, changes in histone acetylation and methylation were found to alter the expression of genes involved in stress response and metabolism, ultimately leading to reduced seed viability. (Li *et al*. 2018) [31]. Additionally, changes in DNA methylation, which is a type of chromatin modification, can also impact gene expression during seed aging, as I mentioned in the previous answer. DNA methylation can affect the accessibility of DNA to transcription factors, and changes in DNA methylation patterns during seed aging can lead to altered gene expression and reduced seed viability (Bewley and Black, M. (2012) [32].

Overall, chromatin modification is an important process that can impact gene expression during seed aging. Understanding the changes in chromatin modifications during seed aging can help identify strategies to maintain seed viability and vigor during storage.

5. Conclusion

Seed aging is a complex process that involves various biochemical, physiological, and molecular changes. These changes can ultimately lead to a reduction in seed viability and vigor, which can impact seed germination and seedling establishment. During seed aging, there are several changes that can occur, including the loss of membrane integrity, a decrease in protein content, the accumulation of free radicals, alterations in gene expression, the loss of mitochondrial function, and the inability of ribosomes to dissociate. These changes can lead to a variety of biochemical changes, including lipid peroxidation, protein oxidation, changes in sugar metabolism, changes in reactive oxygen species levels, and changes in hormone level. Furthermore, molecular changes can occur during seed aging, including DNA damage, alterations in gene expression, alterations in protein structure and function, changes in the antioxidant system, DNA methylation, and chromatin modification. Understanding the underlying mechanisms of seed aging can help in developing strategies to maintain seed viability and vigor during storage. Overall, the study of seed aging is crucial for improving seed storage techniques, maintaining genetic diversity, and ensuring the sustainability of agricultural production.

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