

Molecular Landscape of Seed Senescence: Dissecting Micro and Macro Molecular Alterations and their Amelioration Strategies

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ABSTRACT Seed senescence, the final stage of seed development, involves intricate molecular processes that transition from nutrient assimilation to nutrient remobilization. As seeds age, macromolecules such as nucleic acids, proteins and lipids undergo catabolism. These nutrients are then exported to other developing plant parts, including new buds, young leaves, flowers, or seeds, ultimately enhancing reproductive success. Researchers have made significant strides in understanding the genetic and molecular mechanisms underlying seed senescence, aided by the identification of senescence-associated genes (SAGs) and functional assessments in model plants like *Arabidopsis thaliana*. This review delves into the molecular mechanisms underlying seed aging, highlighting the roles of gene expression changes, DNA methylation and chromatin modifications. Reactive oxygen species (ROS) and oxidative stress are identified as key factors contributing to cellular damage during seed aging. The regulation of seed senescence involves complex networks, including chromatin, transcription and post-translational processes. Strategies to manipulate seed senescence aim for improved crop yield, quality and performance. The changes that are associated with seed aging & seed ageing/senescence has been reviewed at molecular levels.

Keywords: Seed senescence, DNA methylation, chromatin modification, reactive oxygen species, transcription process, molecular mechanisms

INTRODUCTION

Senescence or biological aging is characterized by the gradual deterioration of functional characteristics in living organisms. The word senescence can refer to either cellular senescence or to senescence of the whole organism. Senescence involves an increase in death rates and/or a decrease in fecundity with increasing age, at least in the later part of an organism's life cycle. Senescence is the inevitable fate of almost all multicellular organisms but it can be delayed by various means [1]. There is no general agreement about what are the boundaries and overlaps between ageing, death, senescence, ripening, post harvest deterioration, hypersensitivity, lesions, chlorosis, necrosis and so on [2]. Seed senescence is the process of aging in seeds, which involves a series of physiological and biochemical changes leading to the deterioration of seed quality and viability [3]. It is the final stage of seed development, where the seed reaches physiological maturity and the flow of nutrients from the mother plant to the seed ceases [4]. This process is irreversible and results in the loss of seed vigour and germination potential

[5]. Seed senescence is crucial in agriculture as it directly impacts crop yield and quality. Understanding and managing seed senescence can help improve seed longevity, storage and overall crop productivity. Managing the changes associated with seed senescence can extend the shelf life of seeds, ensuring they remain viable for planting in subsequent seasons and also delaying seed senescence can lead to higher crop yields, as seeds maintain their vigour and germination potential [6].

SEED SENESCENCE: AN OVERVIEW

Seed senescence is a complex process involving various physiological and biochemical changes. Some key physiological changes during seed senescence include the loss of integrity in food storage cells, degradation of chlorophyll content leading to a loss of green pigmentation and a decrease in starch content which reduces the energy available for the seed [7]. Additionally, there is a reduction in proteins and RNA, affecting the seeds ability to synthesize new proteins and nucleic acids. Photosynthesis ceases, halting energy production and DNase enzymes degrade DNA molecules, impacting genetic integrity.

On the other hand, with respect to biochemical entities, seed senescence involves the accumulation of reactive oxygen species (ROS), leading to oxidative stress and damage to cellular components. Lipids in cell membranes undergo peroxidation, causing membrane damage and there is a loss of membrane phospholipids, compromising membrane integrity [8]. The activity of antioxidant enzymes, such as superoxide dismutase and catalase, reduces and allowing for increased ROS damage. Additionally, there is an increase in the production of volatile compounds, which can be detrimental to seed viability [9]. These physiological and biochemical changes collectively contribute to the decline in seed viability and germination capacity.

Seed aging is a natural and irreversible process that leads to a progressive deterioration of seed quality. Initially, it manifests as a delay in the speed of germination, followed by a gradual loss of viability evidenced by an increase in the percentage of seeds unable to germinate and eventually culminates in the death of all seeds in the lot [8]. The stages of seed ageing are influenced by a complex interplay of genetic and environmental factors.

Genetic factors play a significant role in seed longevity. The genetic makeup of seeds determines their inherent ageing process and ability to withstand deterioration. For instance, seeds with robust genetic traits for antioxidant production and DNA repair mechanisms tend to have longer lifespans. Environmental conditions experienced during seed development and storage also shape seed physiology. Factors such as temperature, humidity and light exposure significantly impact seed aging. Seeds stored at lower temperatures and reduced humidity levels tend to have extended longevity [10]. Additionally, the presence of oxygen in storage environments can lead to the production of reactive oxygen species (ROS), causing oxidative stress and cellular damage.

Further, Phytohormones including abscisic acid, auxins and gibberellins have emerged as prominent regulators of seed longevity. These hormones influence various physiological processes that affect seed ageing, such as the activation of antioxidant systems and the maintenance of cellular integrity. Understanding the interactions between genetic factors, environmental conditions and hormonal regulation is essential for developing strategies to preserve seed quality and viability [11].

MICRO MOLECULAR CHANGES DURING SEED SENESENCE

Seed ageing involves various molecular mechanisms that lead to a decline in seed viability and vigour. The major micro molecular mechanisms involved are gene expression changes, DNA methylation and chromatin modification. In gene expression changes lot of gene expression modification occurs during seed ageing. Genes related to stress responses, metabolism and development are often differentially expressed [12]. For example, studies have shown that genes encoding antioxidant enzymes like superoxide dismutase (SOD) and catalase (CAT) are upregulated in aged seeds to combat oxidative stress. Additionally, genes involved in proline biosynthesis, such as P_5CS_1 , are also affected [13, 14].

In DNA Methylation, where an epigenetic modification takes place that can influence gene expression by altering the accessibility of DNA to transcription machinery. In aged seeds, changes in DNA methylation patterns have been observed, which can lead to the silencing of genes important for seed viability and germination. This epigenetic regulation plays a crucial role in the seeds response to ageing and environmental stresses [8]. Chromatin modifications is also one of the changes that can be observed in which histone modifications plays a significant role in seed ageing. These modifications can affect the structure of chromatin and thereby regulate gene expression. Histone acetylation and methylation can either activate or repress gene expression, impacting the seeds ability to maintain viability over time [12]. These molecular mechanisms are crucial for understanding seed aging and developing strategies to improve seed longevity and quality.

Role of Reactive Oxygen Species (ROS)

ROS, such as superoxide anion (O_2^-), hydrogen peroxide (H_2O_2) and hydroxyl radical (OH) *etc.*, are highly reactive molecules that can cause damage to cellular components. During seed ageing, the production of ROS increases, leading to oxidative stress [15]. ROS can damage cell membrane phospholipids, proteins, carbohydrates and DNA, which ultimately affects seed viability and germination.

Oxidative stress occurs when there is an imbalance between the production of ROS and the seeds antioxidant defence mechanisms. This imbalance leads to the

accumulation of ROS, causing cellular damage and deterioration [16]. Oxidative stress can result in the breakdown of cellular structures, loss of membrane integrity and impairment of metabolic processes. Seeds have antioxidant defence systems, including enzymes like superoxide dismutase (SOD), catalase (CAT) and peroxidases, which help neutralize ROS and mitigate oxidative stress. However, during ageing, the efficiency of these antioxidant systems declines, leading to increased oxidative damage [17]. These mechanisms highlight the importance of managing ROS levels and enhancing antioxidant defences to improve seed longevity and quality thereby reducing seed ageing process.

Specific genes and proteins associated with seed ageing

There are several genes and proteins associated with seed ageing and play crucial roles in maintaining seed viability and longevity. Some of them are DOG1 (DELAY OF GERMINATION 1) where, mutations in this gene are associated with reduced seed dormancy and shortened seed longevity which is contrary to the gene SNL1/2 (SWI-INDEPENDENT3 (SIN3)-LIKE) which are also linked to seed dormancy and longevity [18]. The gene OsALDH7 (Aldehyde Dehydrogenase 7) is related to seed aging tolerance in rice [17]. Whereas, the mutation in the gene OsCAD2 (Cinnamyl Alcohol Dehydrogenase 2) affects seed colour and ageing tolerance in rice. Further, PIMT1 (Protein L-isoaspartyl Methyltransferase 1) is involved in protein repair during seed ageing.

In case of proteins, antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT) and peroxidases, play a critical role in neutralizing reactive oxygen species (ROS) and mitigating oxidative stress, thereby protecting seeds from damage during aging. Heat shock proteins (HSPs) are equally important, as they safeguard seeds from various stressors and prevent damage throughout the ageing process. Late embryogenesis abundant (LEA) proteins contribute by protecting cellular structures during seed desiccation and ageing, ensuring seed viability and longevity. Additionally, lipocalins are involved in lipid transport and protection, further supporting seed integrity during ageing. These proteins collectively enhance the seed's resilience and longevity by addressing various stress factors [8]. These genes and proteins are essential for understanding the molecular mechanisms of seed ageing and developing strategies to reduce seed senescence and improve seed longevity.

CHANGES IN MACROMOLECULES DURING SEED AGING

Lipid peroxidation is a critical event in seed ageing. It involves the oxidative degradation of lipids, leading to the production of malondialdehyde (MDA) and other reactive aldehydes. These compounds can further damage cellular components, exacerbating the ageing process. The loss of membrane integrity due to lipid peroxidation results in increased membrane permeability, which disrupts cellular homeostasis and impairs seed germination. Although, protein oxidation occurs as a result of reactive oxygen species (ROS) attacking amino acid residues. This leads to the formation of carbonyl groups on proteins, which can alter their structure and function. Oxidized proteins often lose their enzymatic activity, which is crucial for metabolic processes. Additionally, the accumulation of damaged proteins can interfere with normal cellular functions, contributing to the decline in seed vigour. Further, DNA damage is a significant consequence of seed ageing. ROS can cause single and double-strand breaks, base modifications and cross-linking in DNA [19]. These alterations can disrupt genetic integrity, leading to mutations and impaired gene expression. RNA, being more prone to oxidative damage due to its single-stranded nature, can also be affected, further impacting protein synthesis and cellular function [18]. The impact of these molecular changes that significantly impairs seed viability and germination potential. The deterioration of cellular structures and functions leads to reduced energy metabolism, which is essential for the growth and development of the seedling. The compromised membrane integrity affects nutrient and water uptake, further hindering germination. Oxidative damage to proteins and nucleic acids disrupts vital biochemical pathways, resulting in delayed or incomplete germination. Understanding these processes is crucial for developing interventions to enhance seed longevity, such as improved storage conditions and seed treatments [12].

AMELIORATION STRATEGIES

Approaches to delay seed senescence and improve seed longevity

Current strategies to delay seed senescence and improve seed longevity include seed priming, the use of antioxidants and genetic modifications. Seed priming involves partially/controlled manner of hydrating seeds to initiate metabolic processes without allowing full germination, enhancing germination rates, seedling

vigour and stress tolerance. Common methods include hydro-priming (soaking seeds in water), osmo-priming (using osmotic solutions to control water uptake), hormonal priming (using plant hormones to improve germination) and microbial priming (using beneficial microbes to enhance seed performance) [20, 21]. These presowing seed treatments also helps in enhancing seed germination and field stand [22]. Antioxidants help mitigate oxidative stress in seeds, thereby delaying senescence and extending longevity. Common antioxidants used include ascorbic acid (Vitamin C), tocopherols (Vitamin E), selenium and phenolic compounds [17]. Genetic modifications aim to enhance seed longevity by altering genes associated with senescence and stress responses. Techniques include overexpression of antioxidant enzymes to bolster the seeds natural defence mechanisms against oxidative stress, manipulation of senescence-associated genes (SAG's) to modify the onset and progression of senescence and the introduction of stress-responsive genes to improve seed tolerance to abiotic stresses such as drought and salinity [13]. These strategies collectively contribute to improved seed performance and longevity, ensuring better crop yields and sustainability [23].

Advances in omics technologies (genomics, transcriptomics, proteomics, metabolomics) and their role in mitigating seed senescence

Recent advances in omics technologies, including genomics, transcriptomics, proteomics and metabolomics, have significantly enhanced the understanding of seed senescence and provided new avenues for mitigating its effects. Genomics has enabled the identification of key genes involved in seed ageing, allowing researchers to pinpoint genetic markers associated with longevity and stress tolerance [24]. Transcriptomics has shed light on the gene expression patterns during seed ageing, revealing the regulatory networks that control senescence-related processes. Proteomics has helped identify proteins that change in abundance during seed ageing, providing insights into the molecular mechanisms underlying senescence [25]. Metabolomics has allowed for the comprehensive profiling of metabolites, helping to elucidate the metabolic pathways affected by ageing and stress. Together, these omics technologies offer a holistic view of the complex biological processes involved in seed senescence, paving the way for the development of strategies to improve seed longevity and germination potential [26].

FUTURE DIRECTIONS

Gaps in current knowledge and areas for future research

Despite these advances, significant gaps in the understanding of seed senescence remain. A comprehensive understanding of the intricate molecular mechanisms driving seed senescence is still lacking. The specific roles and interactions of various molecular pathways and their cumulative effects on seed viability need further elucidation. Moreover, the role of epigenetic modifications such as DNA methylation and histone modifications in influencing gene expression and seed longevity is not fully understood, necessitating more detailed studies. Additionally, the interaction between genetic factors and environmental conditions in determining seed longevity is complex and not fully characterized. Understanding how different environmental stressors influence the genetic regulation of senescence could lead to better strategies for seed preservation. Furthermore, the role of seed-associated microbiomes in ageing and longevity is an emerging area of interest, but the mechanisms by which these microbiomes influence seed health and ageing processes are still largely unknown. Integrative approaches that combine genomics, transcriptomics, proteomics and metabolomics to provide a systems-level understanding of seed ageing are still in their infancy. More comprehensive studies utilizing these technologies together could offer new insights into the regulatory networks involved and identify novel targets for intervention [24, 26].

Future research should focus on mapping the comprehensive molecular networks involved in seed senescence, investigating epigenetic modifications as targets for improving seed longevity, developing transgenic seeds with enhanced antioxidant capacities and stress tolerance, exploring the potential of seed microbiome engineering to promote seed health and conducting integrated omics studies to build a holistic picture of the seed ageing process. Addressing these gaps will pave the way for more effective strategies to mitigate seed senescence, improve seed longevity and ensure better agricultural productivity and sustainability.

CONCLUSION

The review on seed senescence has explored various molecular mechanisms, including gene expression changes, DNA methylation and chromatin modifications.

These processes are pivotal in driving seed ageing process, with reactive oxygen species (ROS) and oxidative stress playing a significant role in damaging cellular components, leading to reduced seed viability and germination potential. Specific genes and proteins associated with seed ageing, such as antioxidant enzymes (SOD, CAT), heat shock proteins (HSPs), late embryogenesis abundant (LEA) proteins and lipocalins, were identified for their crucial roles in mitigating oxidative stress and maintaining seed health. Changes in macromolecules like lipids, proteins and nucleic acids were highlighted, demonstrating how oxidative damage and molecular alterations impact seed viability. To combat seed senescence, various strategies were discussed, including seed priming techniques (hydro-priming, osmo-priming, hormonal priming, and microbial priming), the use of antioxidants (ascorbic acid, tocopherols) and genetic modifications aimed at enhancing stress tolerance and longevity. Furthermore, recent advances in omics technologies, were emphasized for their role in understanding the intricate molecular networks involved in seed ageing.

Emerging technologies and approaches, such as cold plasma treatment, machine learning for optimizing priming parameters, gene editing tools like CRISPR-Cas9 and advanced imaging techniques, were also helpful in addressing seed senescence effectively. Continued research in the field of seed senescence is crucial for improving crop productivity and sustainability. Understanding the molecular mechanisms and identifying key genes and proteins involved in seed ageing can lead to the development of targeted interventions to enhance seed longevity. Other omics technologies and emerging approaches offer new opportunities to mitigate the effects of ageing, ensuring higher seed quality and better germination rates. By focusing on these research areas, we can develop more resilient crop varieties capable of withstanding environmental stresses and maintaining viability over extended periods. This is essential for ensuring food security and sustainability in the face of changing climatic conditions and increasing global population. Continued investment in seed science will overlay the way for innovative solutions that support agricultural productivity and contribute to a sustainable future. By leveraging these emerging technologies and approaches, researchers can develop more effective strategies to mitigate seed senescence, improve seed longevity and ensure better agricultural productivity and sustainability.

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