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Unraveling the Molecular Basis of Seed Viability and Longevity through Integrated Proteomic and Metabolomic Approaches

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ABSTRACT

This review considered the key factors that regulated seed viability, including environmental conditions and genetic effects and the molecular processes involved during seed storage and germination. Proteomics and metabolomics were key technologies for investigating the molecular properties of seed biology and clarify the mechanisms underlying seed longevity. It underlined the importance of regulatory networks and signaling pathways in seed survival determination. Proteomics employs methodologies like 2D-PAGE and LC-MS/MS to detect stress-responsive proteins and storage proteins that altered with age and desiccation. Metabolomic profiling on GC-MS, LC-MS and NMR explained the roles of primary and secondary metabolites, including antioxidants, sugars and lipids, in seed longevity. Multi-omics approaches gave a deep understanding of seed viability through proteomics and metabolomics combined together, as evidenced by case studies that highlighted the benefits of this integrative method. This review examined storage conditions such as temperature, moisture and availability of oxygen levels on seed proteins and metabolites and the role of desiccation and subsequent rehydration towards seed viability. It examined species-level variations in proteomic and metabolomic profiles among different crop seeds, with a special focus on new adaptations in short-lived or high-value species. In addition, the capacity of proteomics and metabolomics in generating seeds with longer lifespans and the establishment of molecular markers to determine seed quality was addressed. The advent of new technologies and the combination of genomics and transcriptomics promise to further accelerate our knowledge and applications in precision agriculture and food security. Regardless of data interpretation problems, such advances offered great prospects for enhancing seed quality and crop yields.

KEYWORDS: Seed longevity, proteomics, metabolomics, molecular, storage

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1. INTRODUCTION

Seed viability and longevity are essential factors influencing the success of crop production. Viability refers to capacity to germinate and develop into a healthy seedling under ideal conditions, whereas longevity refers to ability to remain viable. These traits are crucial to the quality of crop production systems in modern agriculture, where the demand for high-yielding, stress-tolerant and nutritionally rich crops is rising (Bewley et al., 2013; Huo et al., 2025). High viability ensures that a higher percentage of seeds germinate, leading to lower waste and better resource use efficiency in terms of water, nutrients and labour (Finch-Savage and Bassel, 2016). Also, seeds are more resistant to environmental stresses during germination, which is desirable in regions exposed to unfavorable climate conditions. For instance, rapid and even germination is crucial for wheat, rice, lettuce, carrot and tomato crops, since delayed emergence leads to uneven crop stands and reduced market value (Bradford and Trewavas, 1994). Seed longevity is essential in maintaining seed quality throughout storage and transport. Long-term storage of seeds is a common phenomenon in crop seed supply chains, where seeds have to remain viable for a period of months or even years prior to use. Maintaining the longevity of seeds enables farmers to acquire seeds with high germination potential regardless of the storage period. The genetic makeup of seeds also plays an important role in determining their longevity and viability (Ramtekey et al., 2022). Seed technology innovations such as seed coating, priming and genetic improvement have contributed a lot towards enhancing these qualities in crops (Devika et al., 2021; Kaur and Gupta, 2005). Increased seed longevity is particularly crucial for hybrid vegetable seeds, which are often expensive and need particular storage conditions to be kept vigorous (Chen et al., 2019; Naik et al., 2023). Low-quality seeds, with low viability or longevity, can result in lower yields, higher costs of production and higher dependency on fertilizers and pesticides (Devika et al., 2021). Furthermore, loss of viability during storage represents an problem for seed banks and conservation efforts interested in the conservation of genetic variation in various crops. As an example, scientific efforts have gone into formulating seed storage regimes for peppers and onions in order to secure availability of the two crops in generations to come (Finch-Savage and Bassel, 2016). Proteomics, provides understanding in protein expression, modification and interaction, facilitating identification of crucial regulatory proteins of seed maturity and desiccation tolerance. Using proteomic methods, scientists are able to monitor differences in protein expressions associated with seed vigour, dormancy, and responses to abiotic stresses (Wang et al., 2018, Job et al., 2005). Similarly, metabolomics, the study of metabolites in seed tissues, identifies metabolic pathways important for seed quality and health (Rajjou et al., 2006). Metabolomic profiling offers a comprehensive picture of metabolic changes that take place during seed dormancy, germination and subsequent development (Tinte et al., 2021). Together, these omics technologies give an integrated picture of seed physiology by relating gene expression, protein activity and metabolic change in response to environmental signals. Proteomics and metabolomics also used for the identification of biomarkers for seed quality, crop breeding programs to enhance seed performance and tolerance (Kajrolkar et al., 2025). These methods help in deconstructing the molecular processes that govern seed reaction to stresses like drought, salinity and temperature, enhancing seed tolerance in fluctuating climates (Huo et al., 2025). The combination of proteomics and metabolomics enables scientists to understand seed biology, which is crucial in enhancing agricultural production and yield. Thus, this review considered the key factors that regulated seed viability, including environmental conditions and genetic effects and the molecular processes involved during seed storage and germination.

2. ENVIRONMENTAL AND GENETIC FACTORS AFFECTING SEED LONGEVITY

The seed longevity of crops is influenced by a combination of genetic and environmental factors. Temperature, humidity, light, and storage conditions have a significant impact on seed viability over time. Seeds stored in cooler and drier conditions tend to have longer periods of viability compared to those stored in warmer and more humid conditions. Temperature is also critically important during seed maturation and storage, since higher temperatures will accelerate metabolic processes that result in a decrease in the quality of the seeds. Similarly, moisture content is a critical factor here, with seeds possessing higher moisture content having a greater potential for microbial spoilage and oxidative damage. Apart from the environment, however, genetic factors also play a major role in the longevity of the seed. Certain plant species and cultivars exhibit innate genetic variation that determines their ability to withstand aging and environmental stresses. Genetic factors such as seed coat morphology, biochemical composition and antioxidant function are crucial for seed ability to survive drying and remain viable for longer durations (Devika et al., 2021). Moreover, seed priming and pre-storage treatments have the potential to influence seed longevity by increasing stress resilience and maximizing metabolic processes (Naik et al., 2023). For example, pre-conditioning seeds with regulated hydration or osmotic agents has the potential to increase their storage adaptability and longevity. Understanding the interaction between environmental conditions and genetic characteristics is crucial for the development of improved seed storage technologies and sustainable crop production in various climates.

3. REDOX HOMEOSTASIS FUNCTION IN SEED LONGEVITY

Maintaining redox homeostasis balances the oxidative stress theory of ageing and extends seed lifetime and stored viability. An accumulation of reactive oxygen species (ROS) over time damages cells and degrades seed integrity (Bailly, 2004). Seeds, particularly during dry storage, achieve a delicate balance of ROS production and elimination. ROS and oxidative damage to proteins, lipids, and nucleic acids need to be detoxified by enzymatic superoxide dismutase (SOD), catalase (CAT), as well as ascorbate peroxidase (APX), and non-enzymatic antioxidants like glutathione and ascorbate (Kranner et al., 2006). Job et al. (2005) reported proteomic studies revealing multiple redox-regulated proteins whose expression diverged greatly due to ageing and storage of the seed. In order to enhance seed longevity, thiol-disulfide exchange, glutathionylation, and redox-sensitive transcription factors appear to have to be regulated. Consequently, redox homeostasis controls the complex web of seed ageing and viability and also acts as a defence mechanism (Figure 1).

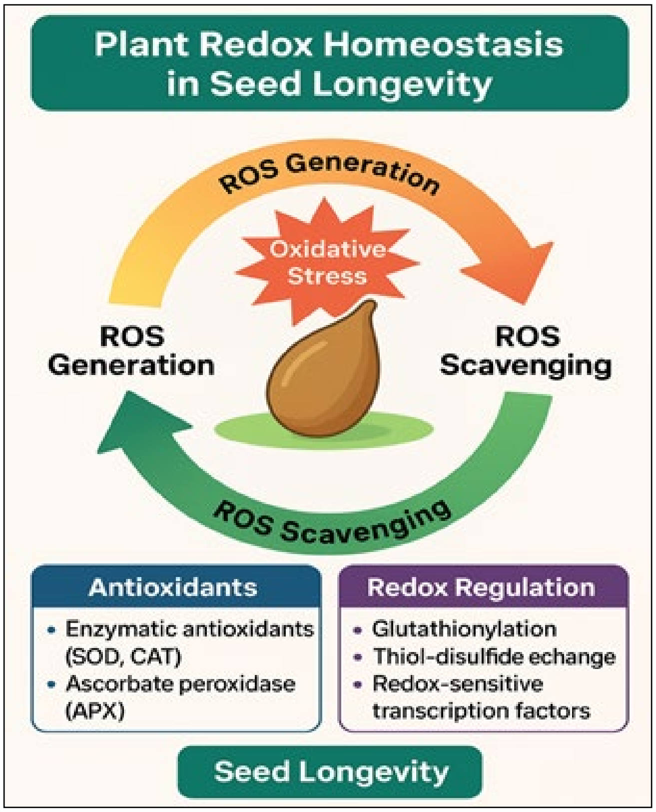

Figure 1: Redox homeostasis in seed longevity includes a balance between ROS generation and scavenging. Antioxidant systems and redox-regulated mechanisms defend cellular components, preserving seed viability throughout storage

4. MOLECULAR BASIS OF SEED VIABILITY AND LONGEVITY

Gene expression during seed storage and germination is a dynamic process that greatly impacts seed longevity, viability and successful germination. During storage, seeds tend to be in a dormant state, with little gene activity. However, many molecular and biochemical processes still operate at low levels to maintain seed integrity from damage due to desiccation and other environmental stresses (Holdsworth et al., 2008). The regulation of storage protein synthesis, including globulins and albumins, is critical during storage, ensuring nutrients are preserved for later use during germination (Bewley et al., 2013). With seed imbibition and the start of germination, gene expression sharply increases, indicating a shift from dormancy to active growth. This process is supported by the breakdown of stored macromolecules such as starches, proteins, and lipids, which supply energy and components necessary for the developing seedling (Bentsink and Koornneef, 2008). The activation of numerous genes related to carbohydrate metabolism, including amylases and sucrose synthases, is vital for transforming stored starches into available sugars. In addition, the expression of genes involved in the loosening and elongation of cell walls, such as expansins, is essential for the emergence of the radicle and the initial growth of the seedling. Simultaneously, environmental factors like light, temperature, and moisture influence gene expression during germination. Transcription factors such as ABA (abscisic acid) and GA (gibberellin) receptors control the balance between germination and dormancy, where ABA inhibits and GA induces germination (Catusse et al., 2008; Koornneef et al., 2002). The complex interaction among these hormonal pathways is important for successful seed germination and seedling establishment. Moreover, the significance of epigenetic changes, such as DNA methylation and histone modifications, is becoming increasingly recognized in seed storage and germination gene expression control. These changes have the potential to affect the seed response under stress and seed quality during storage. In summary, gaining an understanding of molecular mechanisms regulating gene expression in seed germination and storage is essential for the enhancement of seed quality, longevity and environment stress tolerance, particularly in the context of shifting climate regimes.

5. ROLE OF REGULATORY NETWORKS AND SIGNALING PATHWAYS

Regulatory networks and signaling pathways are imperative to maintaining cellular homeostasis and modulating cellular processes, such as growth, development, and reaction to environmental cues. These networks constitute intricate protein, RNA, and small molecule interactions that allow the cell to detect and act upon internal and external cues. Signal transduction pathways, typically activated by extracellular stimuli like hormones or stressors, facilitate such cellular responses by propagating signals to specific cellular targets. Such pathways comprise receptors, secondary messengers, and many downstream effectors that coordinate cellular outcomes (Kaur and Gupta, 2005; Holdsworth et al., 2008). The strongest-documented evidence for signaling includes the plant hormone abscisic acid (ABA), playing a critical role in seed dormancy control and drought resistance. Thorough investigations of ABA signal transduction cascades confirmed that protein kinases, phosphatases, and ABA receptors have an extensively regulated cooperation in order to adjust gene expression during water deprivation (Bentsink and Koornneef, 2008; Nonogaki, 2014). In addition, nitrogen-activated protein kinase (MAPK) pathways, which are involved in stress responses, allow for processes such as programmed cell death and senescence (Huo et al., 2025). These pathways influence cellular destiny as well as intermingle with other signaling pathways in order to combine several signals and elicit a proper physiological response (Bradford and Trewavas, 1994). Signaling network integration plays a critical role in managing stress responses, particularly in plants under varied abiotic stresses like drought, salinity and temperature stress (Leymarie et al., 2012). These stresses trigger cascades of signaling involving transcription factors and post-translational modifications. For example, studies on heat shock proteins (HSPs) have highlighted the role of stress signal pathways in modulating the expression of these proteins to protect cellular structures under heat stress. Moreover, interaction between regulatory networks enables plants to fine-tune their response optimally by toggling between defense and growth (Fu et al., 2024; Finch-Savage and Bassel, 2016). Apart from environmental stress, development processes are equally tightly regulated through signaling networks as well. The auxin signaling pathway, for example, regulates plant pattern formation and growth by regulating auxin response factors, which can regulate gene activity for cell division and elongation. Such developmental and stress response networks complementing each other enable plants to thrive in an evolving environment as well as to retain overall vigour. Appreciating the functionality of regulatory networks as well as signal pathways becomes imperative to enhancing methods of improving crops and working toward the improvement of stress-resilient varieties of crops. Continuation research work on the complicated molecular pathways shall bring light about the functionalities enabling adaptation as well as plant resilience (Huo et al., 2025; Tinte et al., 2021).

6. SEED PROTEIN POST-TRANSLATIONAL MODIFICATIONS (PTMS)

During seed development and senescence, PTMs are crucial biochemical processes that manage protein activity, stability, location and relationships. Seed vitality and biology largely depend on PTMs including phosphorylation, carbonylation, glycosylation and ubiquitination (Rajjou et al., 2008). Carbonylation is a chemical marker for seed degeneration frequently induced through oxidative stress (Nguyen et al., 2015). Phosphorylation events have also been associated with stress-responsive pathway activation, which enhances desiccation tolerance and longevity (Smolikova et al., 2020). Proteomic advancements facilitating the mapping of PTM landscapes in seed development and storage reveal how significant these changes are in seed stress responses and energy metabolism (Arc et al., 2011). Acquiring knowledge about PTMs offers a potential avenue to enhance seed vigor through precision breeding and biotechnology approaches.

7. PROTEOMIC TECHNIQUES USED IN SEED BIOLOGY RESEARCH

Proteomics is an important tool in seed biology studies to explore the complex molecular mechanisms regulating seed development, germination, dormancy and stress tolerance. Among numerous proteomic methods, two-dimensional gel electrophoresis (2D-PAGE) and liquid chromatography-tandem mass spectrometry (LC-MS/MS) are widely employed for seed proteome analysis. 2D-PAGE is an old method that separates proteins based on their isoelectric points and molecular weights, allowing researchers to see protein expression patterns and identify changes in response to environmental stress or genetic modification. This technique has been widely applied to identify proteins involved in seed germination and dormancy (Qin et al., 2021; Job et al., 2005). Despite these, 2D-PAGE also has limitations like poor resolution for acidic or basic proteins and not being able to analyze low-abundance proteins. To overcome these limitations, LC-MS/MS is now the preferable technique because it is highly sensitive and can analyze complex mixtures of proteins without electrophoretic separation in advance. LC-MS/MS integrates the advantages of liquid chromatography for separating proteins with mass spectrometry for identifying and quantifying them (Rajjou et al., 2006). This method has been applied to various seed species to examine proteomic alterations during seed maturation, storage, and their responses to abiotic stresses like drought and salinity (Finch-Savage and Bassel, 2016; Kajrolkar et al., 2025). One of the most important advantages of LC-MS/MS lies in its ability to identify post-translational modifications (PTMs) of seed proteins, which are responsible for regulating protein function and stability in response to environmental stimuli (Huo et al., 2025). In addition, mass spectrometry-based approaches enable high-throughput, large-scale proteomics, which in turn facilitates the identification of stress tolerance and seed quality-related biomarkers (Tinte et al., 2021). Integration of proteomic information with transcriptomics and genomics provides a comprehensive view of the molecular processes involved in seed biology. Proteomic methods, particularly 2D-PAGE and LC-MS/MS, are essential for studying seed biology because they provide important insights into seed physiology, stress tolerance, and quality-improvement tactics. Further developments in these technologies will allow for the creation of more stress-resistant crop varieties and offer deeper insights into seed biology (Table 1 and 2).

8. IDENTIFICATION OF STRESS-RESPONSIVE AND STORAGE PROTEINS AND IT'S MODIFICATIONS DURING AGEING AND DESICCATION

For an understanding of plant response to environmental stress and ageing, there is a need to identify stress-responsive proteins for storage and protein changes during ageing and dehydration. Particularly in stressful conditions like drought, excessive salt and extreme fluctuations in temperature, proteins play a key role in cellular existence and functioning (Kaur and Gupta, 2005). Desiccation has been studied extensively in seeds and other stress-tolerant tissues because it is a condition where water loss causes cell damage, negatively affecting protein structure and function. Understanding the alterations to the proteome that occur under this process is important for developing

Table 1: List of proteomics methods as biotechnological tools for crop improvement in different major crops

Major crops	Proteomic Method	Trait or condition investigated	Tissue/Plant part studied	Reference
Rice	2-DE	Response to selenium treatment	Leaf tissues under micronutrient stress	Gong et al., 2012
	2-DE	Somatic and zygotic embryogenesis	Developing embryos at early stages	Zi et al., 2012
	Shotgun proteomics	Grain development dynamics	Developing grains at multiple stages	Lee and Koh, 2011
	2-DE	Heat stress effects	Spikelet tissues during flowering stage	Jagadish et al., 2010
	2-DE	Drought induced responses	Peduncles during reproductive growth under drought	Muthurajan et al., 2011
	iTRAQ	Cold stress adaptations	Leaves at seedling stage exposed to low temperatures	Neilson et al., 2011
Soybean	2-DE	Phytophthora resistance	Hypocotyl tissues during early infection	Zhang et al., 2011
	2-DE, Blue Native PAGE	Response to submergence	Roots and hypocotyl tissues under anaerobic stress	Komatsu et al., 2011
	2-DE	Oxidative damage and recovery	Fully expanded leaf tissues	Galant et al., 2012
	2-DE	Heat-induced protein response	Mature leaves exposed to elevated tempera-ture	Wang et al., 2012
	iTRAQ	Enhanced nutrient and water uptake (rhizobia inoculation)	Root tissues post-Bradyrhizobium symbiosis	Nguyen et al., 2012
Wheat	2-DE	Response to desiccation	Embryo tissues during dehydration	Irar et al., 2010
	iTRAQ and 2D-DIGE	Drought stress adaptation	Mature leaf blades under water deficit conditions	Ford et al., 2011
	2D-DIGE	Salt stress response	Fully expanded leaves exposed to salinity	Gao et al., 2011
	2-DE	Senescence and oxidative stress	Stem tissues at different aging stages	Bazargani et al., 2011

Table 1: Continue...

Major crops	Proteomic Method	Trait or condition investigated	Tissue/Plant part studied	Reference
Maize	2-DE	Response to water-logging	Root tips and elongation zones under flooding	Kong et al., 2010
	2-DE	Post-anthesis metabolic changes	Amyloplasts isolated from developing endosperm	Dupont, 2008
	2-DE	Fusarium head blight infection	Developing kernels post-infection	Foroud et al., 2008
	2-DE	Heat stress impact	Kernel tissues un-der high tempera-ture	Laino et al., 2010
	2-DE	Unintended effects of genetic modification	Leaf tissues from GM and non-GM plants	Barros et al., 2010
	nanoLC-LTQ-Orbitrap	Leaf morphogenesis in C4 photosynthesis	Developing photosynthetic leaf blades	Majeran et al., 2010
	2-DE	Desiccation response	Embryonic axes during dehydration	Huang et al., 2012
	Shotgun proteomics	Photosynthetic machinery	Thylakoid mem-brane proteins from chloroplasts	Liu et al., 2011
	Shotgun proteomics	Desiccation stress	Embryo tissues during rehydration	Amara et al., 2012
	2-DE	Drought tolerance	Xylem sap collected from roots and stem regions	Alvarez et al., 2008
	iTRAQ	Response to fungal ear rot	Developing ear tissues post-infection	Mohammadi et al., 2011

Table 2: List of PTMs proteomics in crops

PTMs	Crop	Plant tissue used	PTM detection method	MS	No*	Major findings	Reference
Post-translational glycosylation Glycosylation	*Phaseolus vulgaris* (Common bean)	Leaf tissue of mature plants	Qproteome Total Glycoprotein Enrichment Kit (Qiagen)	Liquid Chromatography coupled with Tandem Mass Spec-trometry (LC-MS/MS)	35	Elevated be-ta-glucosidase levels observed among proteins in-volved in cell wall metabolism.	Zadražnik et al., 2017
	Triticum aestivum (Common Wheat)	Fully Expanded leaf tissue	Protein enrichment using Hydrophilic Interaction Liquid Chromatography (HILIC) to enhance detec-tion of glyco-sylated pro-teins	High-resolution Liquid Chromatography coupled with Tandem Mass Spec-trometry (LC-MS/MS)	A total of 173 unique glycosylated proteins were detected and quanti-fied	Drought stress influenced the abundance of glycosylated proteins, many of which are linked to key physiological processes such as signal perception and transduction via protein kinase pathways, and modifications in plant cell wall composition and architecture	Chang et al., 2021

Table 2: Continue...

PTMs	Crop	Plant tissue used	PTM detection method	MS	No*	Major findings	Reference
Phosphorylation	Rice (*Oryza sativa*)	Isolated proto-plast cells	Proteins enriched using a HIS-kinase buffer, followed by immunoprecipitation with anti-FLAG antibody	Liquid Chromatography-Tandem Mass Spec-trometry (LC-MS/MS)	152	The cyclic-nucleotide-gated channel protein OsCNGC9 was found to play a vital role in im-proving rice tol-erance to chilling by controlling cold-induced Ca^{2+} signaling	Wang et al., 2021
	Tomato (*Solanum lycopersicum*)	Mature leaf tis-sues	Protein phosphorylation sites were enriched using the PolyMAC-Ti kit targeting phosphopeptides	Liquid Chromatography-Tandem Mass Spec-trometry (LC-MS/MS)	550	SnRK2 kinases and their directly phosphorylated substrates were implicated in en-hancing tomato's capacity to en-dure prolonged cold exposure	Hsu et al., 2018
	Maize (*Zea mays*)	Leaf tissues from etiolated seedlings	Proteins were isolated and enriched using nickel–nitrilotriacetic acid (Ni-NTA) beads which bind to phosphotyrosine residues	Liquid Chromatography-Tandem Mass Spec-trometry (LC-MS/MS)	692	Tyrosine phos-phorylation events and calci-um-mediated signaling path-ways were found to be essential during the transi-tion of maize leaves from dark to light (de-etiolation)	Arefian et al., 2021

increased resistance to stress, especially in crops of economic importance (Rajjou et al., 2006). Stress-responding proteins such as dehydrins, heat shock proteins (HSPs), and late embryogenesis abundant (LEA) proteins are responsible for protecting plant cells against drying and other non-biological stresses (Bentsink and Koornneef, 2008). For example, dehydrins are accumulated upon dehydration and assist in protecting cellular structures from the harmful effects of drying. Similarly, HSPs act as molecular chaperones that prevent protein aggregation during heat stress by aiding in the refolding of proteins. These proteins, along with other stress-induced proteins, create a complex network that assists plants in maintaining cellular equilibrium and withstanding damage during stressful conditions (Figure 2).

Storage proteins like globulins and albumins are essential for a plant's survival under stress. It is regarded as nutritive proteins, these storage proteins supply the crucial nutrients and energy for germination and early seedling development. Storage proteins, meanwhile, may be modified during ageing under certain circumstances like desiccation, thereby influencing their efficacy. The instability of storage proteins has been related to a loss in seed vigour as seed ageing progresses. The common thread in all these modifications is oxidative damage. Alterations may render the protein structure incapable of performing its normal biological functions. Afflictions to protein may occur during ageing and desiccation, including oxidation, glycation, and proteolysis. As a result, the cell builds up with damaged or misfolded proteins, inhibiting cellular functions and hastening ageing. Oxidative stress is a key cause of protein damage in desiccation, leading into the occurrence of carbonylated proteins. Those carbonyl groups mostly serve as an indication of protein oxidation, whose increased presence correlates with a decrease in seed quality. Besides oxidative changes, proteolysis during desiccation may lead to the disintegration of both storage and stress-responsive proteins, further compromising cellular stability (Delahaie et al., 2013). Protein changes during desiccation go beyond structural changes; they include the alteration of protein functions as well. For example, desiccation-induced modifications can affect the enzymatic capabilities of proteins within metabolic pathways, which will determine seed viability and ability to grow again after rehydration. The interaction among protective mechanisms, like the synthesis

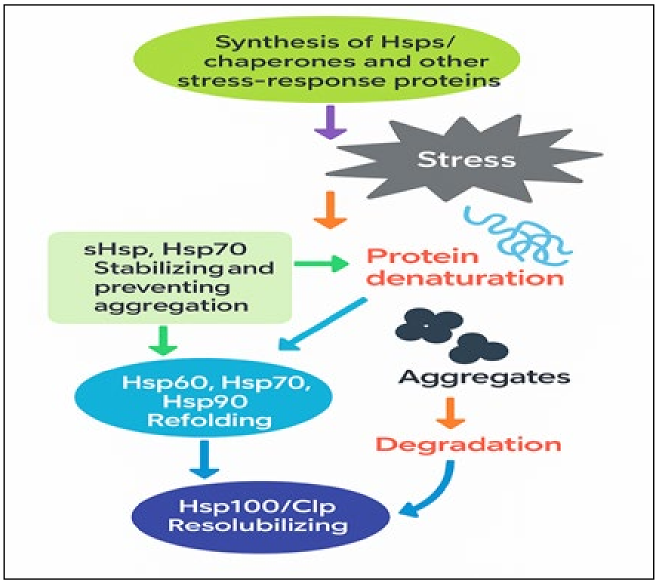

Figure 2: Formal representation of the role of heat shock proteins (Hsps) in cellular stress response and protein homeostasis. Heat shock proteins (Hsps) mediate cellular defense under stress by preventing protein aggregation and assisting in refolding. Denatured proteins are stabilized by sHsps and Hsp70, refolded by Hsp60/70/90, or resolubilized by Hsp100/Clp. Aggregated proteins are either degraded or rescued, maintaining protein homeostasis

of stress-proteins and non-essential protein degradation is vital in surviving desiccation (Finch-Savage and Bassel, 2016). Recent advances in proteomic analyses have enabled the analysis of the alterations in proteins induced by dehydration and ageing (Finch-Savage and Bassel, 2016). Among the techniques used to study specific incidences of protein alterations and measure their functional effects, mass-spectrometric methods have perhaps been the most important. These methods have facilitated researchers in charting the proteomic transformations that occur in seeds during both desiccation and ageing, leading to the identification of potential biomarkers for seed longevity and resilience to stress (Tinte et al., 2021). Gaining an understanding of the distinct functions of these proteins and their modifications offers critical insights for formulating approaches to enhance stress tolerance in crops, particularly those of high commercial value.

9. METABOLOMIC PROFILING TECHNIQUES

Metabolomic profiling techniques, such as Gas Chromatography-Mass Spectrometry (GC-MS), Liquid Chromatography-Mass Spectrometry (LC-MS) and Nuclear Magnetic Resonance (NMR) are widely used for the analysis of metabolites in bio-samples. GC-MS is a strong method of analysis of volatile and semi-volatile compounds, with high sensitivity and very good reproducibility. This technique involves the separation of compounds by gas chromatography, with their identification and quantification by mass spectrometry. It is best at breaking down smaller molecules like fatty acids, amino acids and sugars. Alternatively, LC-MS has benefits when probing thermally labile and polar metabolites. LC-MS couples liquid chromatography to separate molecules with mass spectrometry for detection, thereby allowing identification as well as measurement of a large variety of metabolites, e.g., lipids, peptides, and small molecules. NMR spectroscopy offers a high-resolution, non-invasive technique for metabolomic profiling that provides detailed information about molecular structure and concentration of metabolites in complex biological matrices. It is particularly useful for the study of large biomolecules like proteins and nucleic acids, as well as small metabolite. Each of these methods has specific strengths and weaknesses; however, when used in combination, they provide complementary data that enhance our knowledge of metabolic networks (Tinte et al., 2021). GC-MS is optimally suited to small, volatile compound analysis, LC-MS for complex and polar samples and NMR provides high-resolution structural information. The combination of these methods has propelled advancement in a variety of disciplines, from plant biology and pharmacology to disease diagnosis, and thus they are the primary tools in contemporary metabolomics (Figure 3).

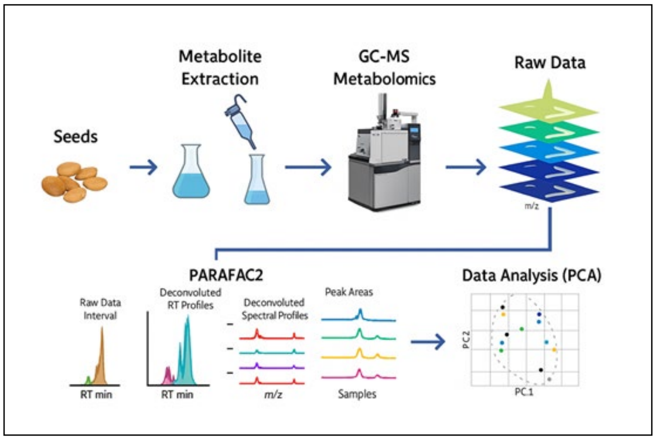

Figure 3: An overview of the metabolomics workflow using GC-MS as apply for the study

10. METABOLITES AND MECHANISMS INFLUENCING SEED LONGEVITY: ANTIOXIDANTS, SUGARS, AND LIPID METABOLISM

Primary and secondary metabolites significantly influence seed longevity through their involvement in metabolic stability and stress tolerance to impart protection to seeds during storage and germination. Primary metabolism that involves secondary metabolites is important in the sustenance of metabolic processes that ensure seed survival during storage and among secondary metabolites, phenolics, alkaloids and terpenoids possess defensive roles in seed longevity (Bewley et al., 2013; Kaur and Gupta, 2005). The functions maintaining seeds from oxidative stress, maintaining the energy reserves and sustaining the membrane integrity, i.e., antioxidant activity, sugar metabolism and lipid metabolism are crucial for long-term survival. Carbohydrates are one of the major seed components, delivering energy to seeds in both dormant and germination stages. Sugars like sucrose, glucose and fructose regulate osmotic adjustment, which stabilizes cellular structures and guards against damage to proteins and membranes. Notably, sucrose plays a role in the synthesis of storage compounds while also providing protection in terms of seed desiccation tolerance, as it helps stabilize cellular structures during the drying process. The buildup of sugars further supports antioxidant systems in seeds by boosting the production of key antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD), which assist in reducing damage caused by reactive oxygen species (ROS) during storage. Lipid metabolism is another vital factor influencing seed longevity. Lipids, especially polyunsaturated fatty acids (PUFAs), are crucial components of seed membranes and their integrity is necessary for seed survival. However, the oxidative degradation of PUFAs can lead to lipid peroxidation, which harms cell membranes and speeds up ageing. Seeds with higher levels of saturated fatty acids, including palmitic acid, are more tolerant to oxidative damage and survive longer. Also, the changes in lipid metabolism may affect the seed's resilience to oxidative stress since fatty acid biosynthesis and degradation enzymes strictly regulate the production and breakdown of lipids (Finch-Savage and Bassel, 2016; Tinte et al., 2021). While secondary metabolites do not directly participate in primary metabolic processes, they also enhance seed longevity by functioning as antioxidants. Phenolic compounds, flavonoids and alkaloids possess antioxidant properties that protect seeds from oxidative stress during storage. The application of amino acids and polyamines using foliar sprays shows an efficient approach to enhancing the tolerance of medicinal plants against saline and drought conditions. Various treatments can enhance better accumulation of photosynthetic pigments, reduce nitrate-nitrogen accumulation and increase the overall quality of production by addressing leaf-related problems (Ismail et al., 2024) (Figure 4).

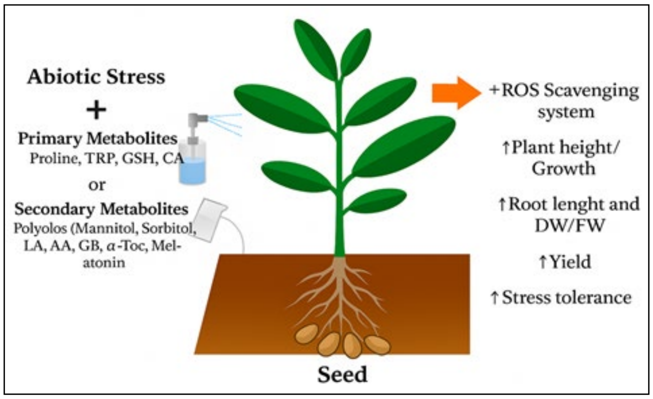

Figure 4: The application of primary and secondary plant metabolites helps reduce the adverse effects of abiotic stress. When these metabolites are applied through foliar sprays or irrigation, they enhance the resilience of crops against environmental challenges

These metabolites will protect seeds against microbial infection as well as abiotic stress that can lower the viability of the seeds. They also regulate the control of defensive responses in plants. For example, longer lifetime of seeds as well as increased resistance to abiotic stress has been linked to the accumulation of phenolic acids, e.g., ferulic acid, during seed maturation. Antioxidants play a critical role in protecting seeds against oxidative harm caused by ROS, which are formed during senescence and seed storage. ROS can damage proteins, lipids and nucleic acids, which reduces the seed viability. Antioxidants like glutathione, vitamin C (ascorbic acid) and vitamin E (tocopherols) scavange ROS and prevent oxidative chains from initiating. Huo et al. (2025) reported that antioxidants also assist cells in keeping their redox balance, which is required to sustain biological activities during dormancy and seed germination. Seeds are controlled by the metabolic status of the developing seed, genetic predisposition, and environmental conditions to possess amounts of antioxidants.

11. SYNERGISTIC INSIGHTS INTO SEED VIABILITY THROUGH MULTI-OMICS APPROACHES

Conventional methods for examining seed viability primarily rely on germination assays and physiological evaluations. Nevertheless, technological advancements have introduced multi-omics strategies, including genomics, transcriptomics, proteomics, and metabolomics, which offer a more comprehensive perspective on the elements that affect seed viability. These techniques facilitate an enhanced understanding of the molecular mechanisms that drive seed maturation, dormancy, and germination processes. Multi-omics methods synthesize information from different molecular levels, providing an all-encompassing overview of seed development, desiccation resilience, and post-germination activities, essential for assessing seed quality and viability (Ramtekey et al., 2022). Genomics, which involves the analysis of an organism's complete genetic framework, has played a crucial role in comprehending seed viability.

Whole-genome sequencing enables the identification of genetic markers linked to seed viability characteristics, including dormancy, vigour, and resistance to environmental stresses (Fu et al., 2024). The sequencing efforts on model organisms like Arabidopsis thaliana have uncovered genes associated with seed coat development, embryo formation, and desiccation resilience, yielding significant insights into the genetic aspects of seed viability. Furthermore, advancements in transcriptomics have highlighted essential genes that govern the signaling pathways connected to seed dormancy and germination (Catusse et al., 2008). By studying RNA expression profiles throughout seed maturation and germination, transcriptomic analyses can identify critical markers for seed viability, such as those involved in abscisic acid (ABA) signaling and hormonal regulation, which are vital in the processes of seed dormancy and germination.

As proteomics reveals all the proteins expressed in an organism, it is easier to understand seed viability better. Proteomics provided direction for the accumulation of proteins related to stress-proteins and enzymes associated with energy metabolism and necessarily structural protective proteins for seeds (Finch-Savage and Bassel, 2016) associated with the protection of desiccation from natural stresses. Proteomic studies have contributed to the identification of protein biomarkers with vigour and germination potential, thereby improving prediction of how seeds will perform in diverse situations. Furthermore, metabolomics the small molecule in small molecular compounds are another important place for study the biochemical pathways affecting seed viability have been in the spotlight. Analysis of individual compounds (e.g., sugars, amino acids and lipids) in seeds metabolites can connect these low molecular weight entities to desiccation tolerance and stress-proness resilience of seeds (Tinte et al., 2021). Such an approach has demonstrated how changes in seed maturation and dormancy metabolism will shift the quality of seeds overall. The combination of these omics offers a more fine-grained understanding of the molecular and biochemical processes involved in seed viability. Combining multi-omics datasets (e.g. genomics, transcriptomics, proteomics and metabolomics) allows a more precise prediction of seed behavior under different environmental conditions facilitating the improvement of seed conservation approaches (Gonzalez et al., 2020).

12. IMPACT OF TEMPERATURE, HUMIDITY, OXYGEN, DESICCATION AND REHYDRATION ON SEED PROTEINS, METABOLITES AND VIABILITY

The relationship between temperature, humidity, oxygen levels, desiccation, and rehydration plays a crucial role in seed proteins, metabolites and overall viability, making it an important focus in seed physiology and storage biology. Temperature is an influential factor that affects seed metabolism. High temperatures cause the denaturation of protein through oxidation, proteolysis and enzymatic reaction decrease (Rajjou et al., 2008). On the other hand, lower temperatures preserve proteins and metabolites stability (which generally favour cold storage closer to keeping viable seeds). Humidity is another essential factor, as high relative humidity can lead to moisture absorption in seeds, initiating metabolic activity that may undermine storage longevity and protein functionality (Bewley et al., 2013). In comparison, decreased humidity raises desiccation tolerance, an important survival response in orthodox seeds. Oxygen levels also influence seed metabolism. Reduced oxygen levels such as those faced during hermetic storage have been shown to repress oxidative stress by limiting the production of reactive oxygen species (ROS). This reduction helps maintain seed proteins and essential metabolites important for germination (Chen et al., 2019). Prolonged oxygen limitation, however, can negatively affect anaerobic metabolism, resulting in poorer germination vigour. Desiccation, which is a natural process for most seeds, enhances longevity by stopping metabolic processes at low water content. Desiccation tolerance is linked to the storage of late embryogenesis abundant (LEA) proteins and protective metabolites such as sugars and antioxidants, which stabilize cellular structures and protect against damage during drying (Choudhary et al., 2023). Seed rehydration following desiccation initiates a sequence of complex physiological events. Too rapid an intake of water may induce imbibitional damage, leading to membrane impairment and viability reduction. Controlled rehydration enables proteins to regain function and activates metabolic activities associated with seed germination. Proteomic analysis reveals substantial alteration during rehydration, including the activation of stress-response proteins and the enzymes of energy metabolism, which play key roles in seed viability recovery (Figure 5).

13. COMPARATIVE PROTEOMICS AND METABOLOMICS IN HIGH-VALUE AND SHORT-LIVED VEGETABLE SEEDS

Comparative proteomics and metabolomics have emerged as essential new methods for dissecting the differential adaptations of high value short-lived vegetable seeds. The application of such methodologies contributes to the understanding of the molecular and biochemical processes that impact on seed quality, vigour and longevity. Seeds of high value like, hybrid vegetable seeds have huge economic importance as they are responsible for massive yield and good performance of the crop. On the

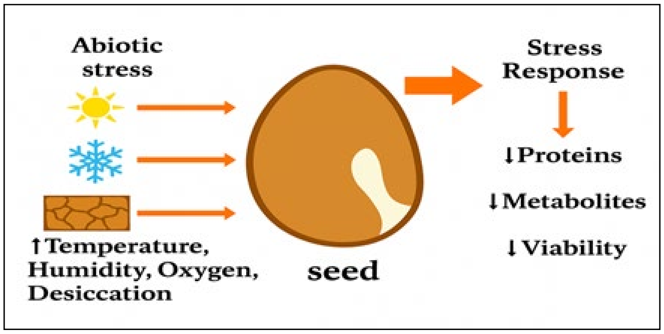

Figure 5: Stresses like Temperature, Humidity, Oxygen, Desiccation reduces seed quality. Environmental stress factors, such as high temperature, heat, high cold, severe drought, high saline elicit stress responses in seeds and reduce photosynthetic activity, proteins, metabolites and viability which ultimately lower seed growth and thus plant germination

other hand, short-lived seeds (e.g. onion and parsley) are particularly prone to rapid deterioration, which is a problem for storage and distribution. Together, proteomics and metabolomics have started to reveal how these seeds behave under environmental and physiological stresses that result in storage as well as germination potential. Proteomics is primarily aimed at the identification and quantification of seed proteins, which are involved in seed storage accumulation, stress tolerance and regulation of metabolism. Comparative proteomic studies have indicated that seeds from high-value crops display unique protein profiles that enhance their ability to tolerate desiccation and manage oxidative stress. For example, research has shown an increased presence of heat shock proteins (HSPs) and late embryogenesis abundant (LEA) proteins in seeds that are tolerant to desiccation (Delahaie et al., 2013). These are necessary to the survival of cellular integrity in storage and drying, as seeds will have lost viability by the time they are processed. If we look at seed longevity, which are generally short-lived seeds show lesser amounts of these protective proteins, which is in accordance with their environmental stress sensitivity. Metabolomics extends proteomics depth with metabolites, the small molecules involved in many cellular processes. Typically, durable vegetable seeds build up metabolites that are antioxidant, osmoprotective, or signalling molecules in an effort to reduce stress on their tissue. In contrast, short-lived seeds are enriched in a more limited set of metabolites that makes them liable for higher lipid peroxidation and metabolic disorder during storage. Understanding such metabolomic distinctions is crucial in order to further improve seed priming techniques and storage conditions. Proteomics and metabolomics integration has also highlighted the impact of genetic and environmental factors on seed adaptations. For example, transcriptomic analysis coupled with proteomic and metabolomic data has exposed how specific genes regulate the production of protein and metabolites in seeds. Such multi-omics approaches may predict markers for seed quality that can be targeted by breeders to design traits associated with longevity and vigour.

14. EMERGING OMICS TECHNOLOGIES

Newly developed omics technologies like genomics, transcriptomics, proteomics and metabolomics have transformed agricultural science, providing novel insights into plant biology, crop enhancement, and food security. These technologies allow for a more accurate understanding of plant functions, aiding in the creation of crops that are more resilient to environmental challenges, diseases, and pests. Through an integration of these omics techniques, researchers will enhance food security and sustainable agriculture, ever more essential with a growing global population and changing climate. Genomics deals with the whole of the genetic content of an organism and provides key information on gene structure, function, and evolution. With the development of next-generation sequencing technologies, genomics has aided in the discovery of significant agronomically related genes such as yield, disease resistance, and drought tolerance. Genomic discovery can be utilized for marker-assisted selection (MAS) and genome editing tools like CRISPR/Cas9 for crop breeding with favourable characteristics, thus improving productivity and agricultural sustainability (Fu et al., 2024). Moreover, genomics can help pinpoint genes involved in plant-pathogen interactions, which is vital for creating crops with improved disease resistance and reducing reliance on chemical pesticides (Smýkal et al., 2015). Transcriptomics, which examines RNA molecules and gene expression, offers a dynamic perspective on gene activity in plants under various environmental conditions. Transcriptomic platforms, such as RNA sequencing (RNA-Seq), offer profound insights into the response of plants to abiotic stresses such as drought, heat, and salinity, as well as biotic stresses due to pathogens (Wang et al., 2018). Decoding of gene expression profiles provides researchers with further insight to determine regulatory networks and core transcriptional master regulators, which are essential for stress-responsive biology that can be exploited to enhance crop resilience (Wang et al., 2009). Further, transcriptomics would provide the molecular underpinning of key traits (flowering time, seed production bunches, ripening fruits etc.), all central for increased crop yield and quality. Proteomics, which is the large-scale study of proteins, complements genomics and transcriptomics by giving insights into the functional biology of plants. This discipline focuses on the identification, quantification, and role of proteins involved in different biological processes.

Through the exploration of the proteome, scientists can discover the biochemical pathways that control plant development, growth, and reaction to environmental stress (Gu et al., 2016). For instance, stress-related protein analysis can identify biomarkers of drought tolerance or pathogen resistance, which will aid in breeding crops that are able to thrive under stressful conditions. In addition, proteomics is able to investigate plant-microbe interactions and recognize proteins that enable symbiotic relationships with soil microorganisms, ultimately resulting in improved nutrient acquisition and soil quality (Naik et al., 2023).

Metabolomics is the systematic study of small compounds, called metabolites-provides essential knowledge about plant biochemistry and their responses to exogenous treatment. Due to its role in growth, defense and stress response, these metabolites are found to be important for plant physiology; that is why metabolomics effective means of explaining it. Mass spectrometry (MS) and nuclear magnetic resonance (NMR) spectroscopy have been used as metabonomic approaches to indicate the alterations of metabolic processes in response to stress for potential biomarkers of drought, salinity stress and disease resistance (Gu et al., 2016). Metabolomics can also be applied to assess the nutritional value of crops for guaranteeing that population food production satisfies their dietary requirements (Naik et al., 2023). The fusion of genomics, transcriptomics, proteomics, and metabolomics, collectively known as multi-omics, presents a comprehensive outlook on plant biology. This systems biology methodology is crucial for enhancing precision agriculture, facilitating the development of crops that are not only higher in yield but also more nutritious and better equipped to withstand climate change and other challenges (Zhang et al., 2022). The integration of these omics technologies in precision agriculture offers data-driven insights that enable more effective utilization of resources like water, fertilizers, and pesticides, resulting in higher yields while reducing environmental impact (figure 6).

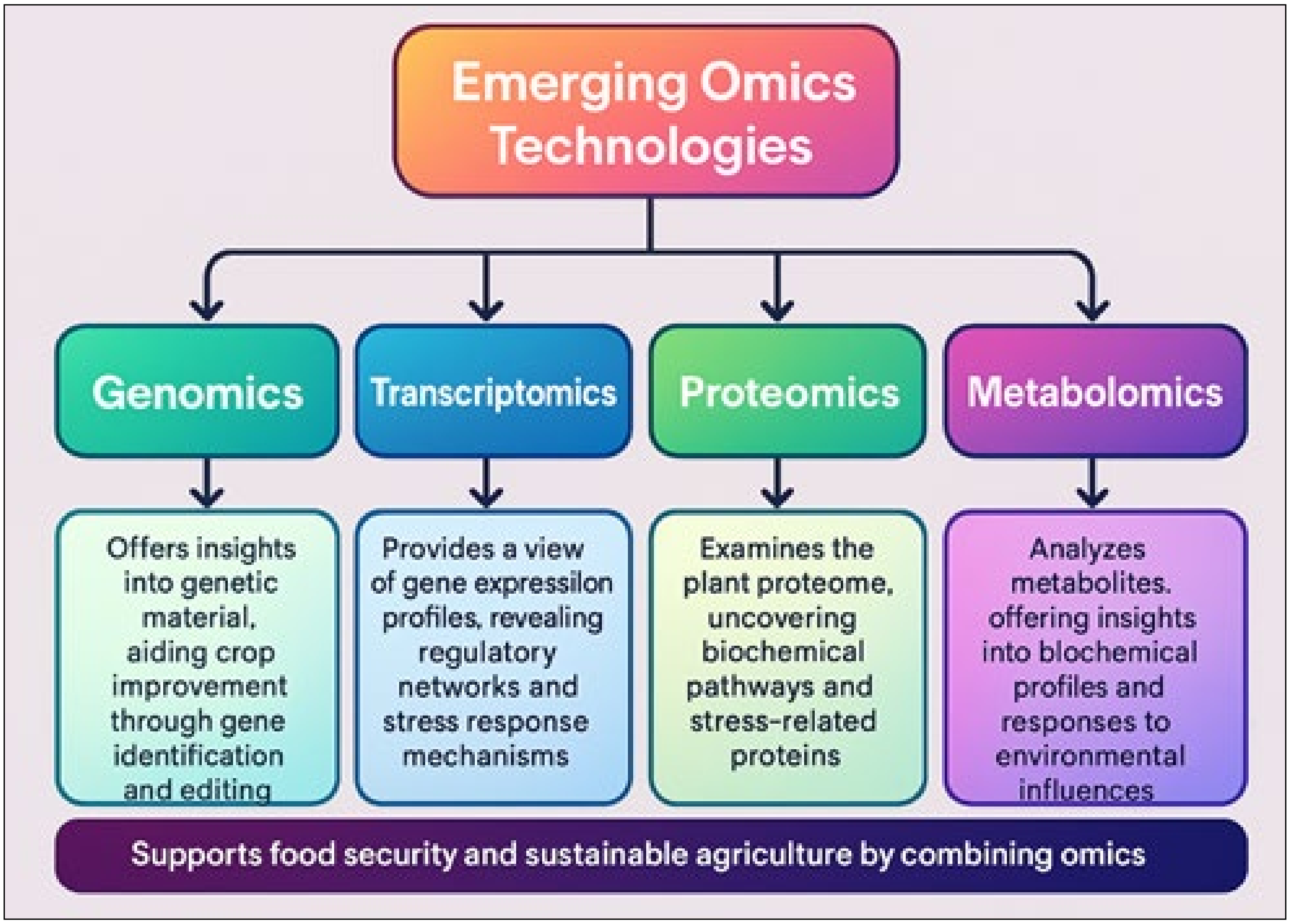

Figure 6: The integration of advanced omics technologies-Genomics, transcriptomics, proteomics, and metabolomics in agricultural research. These interconnected approaches enhance our understanding of plant biology, enabling the development of climate-resilient, high-yielding and nutrient-rich crops for sustainable agriculture

15. IMPLICATIONS FOR VEGETABLE SEED STORAGE AND QUALITY IMPROVEMENT

Seed storage and quality of vegetables need to be maintained in order to have a continuous supply of healthy, viable seeds for planting purposes and food supply. Seeds need to be stored in order to facilitate the survival, ability to germinate and overall quality of the seeds. Seed viability is affected by a variety of different factors, such as moisture content, temperature and storage, all of which must be optimized for the seeds. Poorly stored seeds lead to seed deterioration, which translates to lower germination and hence lower farm production. De Vitis et al. (2020) has indicated that seeds retain their viability best when kept at low moisture content and in cooler environments. Additionally, suitable packaging is important to shield seeds from environmental challenges such as light, humidity and pests (Tiwari et al., 2022). One of the major methods of improving vegetable seed quality is by enhancing the physiological traits of seeds through breeding and biotechnology. It encompasses raising resilience to different biotic and abiotic stresses, such as drought, salinity and diseases. Further, seed treatments such as priming and coating have been established to promote germination under suboptimal conditions and can extend seed shelf life (Devika et al., 2021). Specifically, seed priming entails pre-hydrating the seeds to a precise moisture content, then drying them to a stage where they remain viable, potentially enhancing seed performance during storage and in challenging environmental situations (Thakur et al., 2022). The storage methods required can differ depending on the type of vegetable seed. For example, legumes such as beans and peas have particular storage requirements compared to leafy greens such as spinach or cabbage due to differences in biological composition and metabolic processes. Further, advancements in controlled atmosphere storage-temperature, humidity and oxygen levels are exactly controlled have been found to improve seed viability and enhance the germination capacity of various vegetables. This method is particularly valuable for the long-term storage of vegetable seeds so they can be sown during the next growing season. The improvement of seed storage techniques, better methods for analyzing the seed quality are required to ensure only high-quality seeds are utilized in planting. Methods of seed quality determination, such as measuring percentage germination, seedling vigour and genetic purity, have considerably improved in recent years. The improvements help determine seeds with high chances of success under different environmental conditions. A major part of seed quality improvement is improving seed health to avoid seed-borne diseases that can interfere with germination and seedling emergence of plants. Treatment of seed with fungicides, bactericides or biocontrol agents may alleviate the incidence of seed-borne pathogens and subsequently ensure good seed health as well as ensure seedling establishment success (Devika et al., 2021).

16. CONCLUSION

Proteomics and metabolomics provide valuable information about the molecular machinery of seed longevity, emphasizing protein functions, regulatory and metabolite pathways during storage and germination. Advanced techniques such as 2D-PAGE, LC-MS/MS and GC-MS facilitate in-depth studies of stress-responding proteins and metabolites associated with longevity. The future of seed science lies in the combination of multi-omics with genomics and transcriptomics. The relentless progress of next-generation technologies is set to transform seed science, thus empowering, sustainable agriculture and world food security.

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