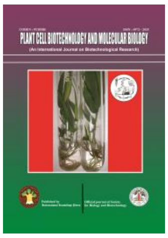

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Mechanism and Methodologies of Seed Priming: Enhancing Germination and Crop Resilience

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

Due to its potential to improve seed germination and early seedling development, "seed priming" has garnered attention recently. This review article covers seed priming systems, their processes, and their many crop production purposes. Seed priming and its importance in seed performance are discussed. Seed priming methods include osmotic, hydro-, hormonal, and microbiological. Each technique is thoroughly detailed, including its procedures, requirements, and pros and cons. The molecular, physiological, and biochemical changes and priming substance-seed interactions of seed priming are examined. The article also discusses seed priming's benefits for stress tolerance, seed germination, seedling vigour, and sustainable agriculture. Most seed treatments use seed imbibition, which allows seeds to germinate but prevents radicals from reaching the seed coat. Dry, desiccation-resistant seeds can be stored until planting. Priming accelerates and synchronises future germination, and early seedlings from primed seeds are often more robust and resistant to abiotic stressors. Progressive farmers that want to boost agricultural productivity would benefit from this technology. This article discusses seed priming methods, mechanisms, and usage in various agricultural situations to boost crop productivity and seed performance.

Keywords: Seed priming; hydro-priming; solid matrix priming; on farm; halo priming; osmoprimimg.

1. INTRODUCTION

India's agriculture industry accounts for 7.8% of GDP, compared to 6.1% globally. Due to population increase and health awareness, there is a huge demand for healthy, appropriate meals eaten at the right times without unacceptable chemicals. Many nations switched to organic or sustainable farming to achieve this. Seed is vital for agriculture's continuing growth because 90% of food crops are grown from seed. Fast germination of high-quality seeds, coordinated seedling development, higher production potential, and productivity are essential in agriculture. Many variables reduce agricultural productivity. Poor stand establishment and seed-borne or early seedling infections impair agricultural yields. To meet needs, sustainable manufacturing technology is needed, but expanding output at the expense of the environment is banned. Pre-sowing practices increase agricultural stand establishment by giving the plant the ability to resist stress without affecting output or the environment. The need for new priming agents and technologies to promote agricultural seed germination and seedling growth is growing. 24 define sustainable agriculture as the efficient use of agricultural resources to meet evolving human needs while protecting natural resources and the environment. Many treatments can improve seed germination, seedling vigour, and crop output. It can also help plants tolerate biotic and abiotic stress, reducing their need of fungicides and insecticides.

Seed priming: Seed priming is a process of regulating the germination process by managing the temperature and seed moisture content and is the most widely used seed invigoration technique to improve field emergence and crop establishment under adverse environmental condition [1]. It is among the most significant techniques for physiological seed improvement. According to 26, it is a hydration therapy for seeds that includes regulated imbibition and stimulation of the pregerminative metabolism (activation), but it prevents radicle emergence. Before the seed loses its ability to withstand desiccation, the hydration treatment is stopped [2]. To prime seeds, immerse them in liquids containing plant hormones or advantageous microbes for a designated duration (Bhowmick., M.K. 2013). Before being stored, distributed, or planted, the hydrated primed seeds can be dried to a safe moisture level. A simple and efficient method for achieving rapid and consistent emergence, strong seedlings, and increased agricultural yields is seed priming [3].

Priming is a method that includes varying the temperature and/or the application of different organic or inorganic compounds to seeds [4]. To prevent radicles from emerging before planting, it involves immersing seeds in various solutions for a certain amount of time under regulated circumstances, and then drying them back to their initial moisture content. This counteracts the negative effects of seed degradation and promotes a number of metabolic processes that enhance the germination and emergence of many seed types, especially those of vegetables, small-seeded grasses, and ornamental plants. Seed priming is regarded as a low-risk, low-cost, high-effectiveness, and simple approach [2].

A brief history of seed priming: Since the dawn of agriculture, man has been in contact with seed physiology and has rapidly discovered that many seeds do not germinate consistently and readily. The ability of a seemingly "dead seed" to resuscitate and, upon germination, form a viable young and vigorous seedling captivated ancient society. Focusing on seed physiology, the Greek Theophrastus (c. 372–287 BC) proposed that the germination process may be momentarily halted. According to the Roman scientist Gaius Plinius Secundus, Roman farmers pre-hydrated their legume seeds before spreading them in order to speed up and synchronize germination.

Mechanism of priming: The complex process of seed germination involves several metabolic processes that lead to the transition from the stored food reserve to the activation phase, during which the radicle and plumule appear [5]. Generally speaking, the seeds go through three stages to absorb water. The first stage, known as the imbibition phase, is characterized by a rapid intake of water due to forces generated by seeds. This phase is characterized by alterations in metabolic processes and the translation process, as well as the repair of DNA and mitochondria [6] The second phase, known as the lag phase, is characterized by a little rise in the fresh weight of seeds due to reduced water absorption. Since this phase is quite active in terms of metabolism and physiology, it is also known as the activation phase.

Physiological and biochemical changes in seeds on priming: Different physiological and biochemical changes in seeds are brought about by priming. It breaks dormancy and synchronizes germination reduces the amount of time needed for imbibitions, hydrolyzes or metabolizes inhibitors, activates enzymes, releases stored food, and promotes the development of embryonic tissue. When it comes to seed metabolism, starch metabolism plays a major role in determining how vigorously seedlings respond to stress. α-amylases catalyze this metabolism by hydrolyzing starch stores into sugars that may be metabolized, giving the growing embryo energy [7,8]. By increasing the activity of α-amylase and dehydrogenase, seed priming can hydrolyze starch macromolecules into smaller, simpler sugars, leading to enhanced respiration and ATP generation. During this process, there is a rise in protease, amylase, and phytotase. Malate synthase and isocitrate lyase, which convert fats into carbs, as well as antioxidant enzymes (POD, SOD, CAT, and GR) that scavenge reactive oxygen species (ROS) are also improved by priming. As a result, the seeds are shielded from lipid peroxidation and oxidative damage to the phospholipids in their membranes, increasing their lifetime [9]. Additionally, it has been observed that primed rice seedlings produce more glycine and accumulate proline, which function as osmotic agents, radical scavengers, and enhance GSH synthesis, respectively, shielding the plants from the oxidative damage caused by cold stress. The increased activity of β-mannanases during priming weakens the endosperm layer and facilitates the emergence of radicles, hence ending thermodormancy [10,11]. Priming also sustains tubulin subunit production in large quantities, which supports cell division and the cytoskeleton [12].

Techniques of priming: Numerous techniques (Hydro-priming, halo-priming, osmo-priming, matrix priming, osmohardening, on-farm priming, hormone or growth enhancer priming, micronutrient seed priming (Nutripriming), biopriming, or treating seeds with microorganisms, such as Pseudomonas aureofaciens, Trichoderma spp., and nanoparticle priming, or coating seeds with nanoparticles (NPs)). for seed priming have been devised to stimulate seeds and mitigate environmental stressors. Water-based priming approaches are distinguished from other pre-sowing treatments by their shared characteristic of partially pre-hydrating seeds and initiating early germination processes in seeds. Numerous factors influence priming efficiency, which is mostly dependent on the kind of treated plant and the method of priming that is used.

2. HYDRO-PRIMING

Hydropriming is one of the oldest practices used for seed invigoration. This practice has been used widely to stimulate the speed, uniformity of emergence and improve the final plant stand [13]. The simplest kind of seed priming is called hydropriming, and it involves soaking seeds in clean water and then re-drying them to their original moisture content before planting. Hydropriming is a long-established method for enhancing seed vigor. Traditionally, it has been employed to accelerate and synchronize seed emergence, as well as to boost the final plant stand [14]. Because it doesn't require the use of any extra chemicals as a priming agent, this approach is both inexpensive and ecologically benign. The primary drawback of hydropriming is the seeds' uncontrollably high water absorption. This is a result of seeds having unfettered access to water during hydropriming, which means that the sole factor influencing the rate of water absorption is the affinity of seed tissue for water.

A method called hydro-priming involves soaking seeds in water, drying them to dehydrate them, and then planting them the next day. This speeds up the germination process and increases the vigor and development of seedling. Hydro-priming on aging chickpea seeds and observed higher dry weight of seedlings and a higher rate of germination. When compared to high vigor seeds, priming enhanced the amount of grains/plant/unit area from low vigor seeds and improved the quality of old and damaged seeds, increasing field productivity. Additionally, it raised the percentage of germination and seedling emergence, which led to the efficient use of resources (soil, light) to produce more grains. Among the treatments, hydropriming led to the fastest germination speed, while it also resulted in the shortest mean germination time and the fewest days to 50% emergence, followed by 25% kunapajala priming [15].

3. SOLID MATRIX PRIMING

Osmopriming is expensive, and there are technical issues with aeration; thus, solid matrix priming (SMP, matriconditioning), which regulates seed water absorption, has been developed as an alternative. Seeds are combined and incubated with a moist solid water carrier for a certain amount of time during solid matrix priming. The seeds are then taken out of the matrix, cleaned, and allowed to dry naturally. Using a solid medium mimics the natural imbibition process that occurs in the soil and helps seeds to hydrate gradually [16]. Materials used as matrices must have certain physical and chemical characteristics, such as low matrix potential, low water solubility, large surface area and water holding capacity, non-toxicity to seeds, and the capability to stick to seed surfaces, in order to effectively complete SMP.

It is commonly known that combining SMP with chemical and biological elements may significantly improve seed performance. In a similar vein, matri conditioning hot pepper seeds with GA_3 improved their quality. Trichoderma viride-treated solid matrix priming increased okra seedling emergence and yield at low temperatures, according to more recently published studies [5].

On-farm priming: Seed priming on a farm, must be hydrated for approximately 12 hours, 17 hours in semi-arid tropical regions, 8 hours or overnight surface dried, and then sown the next day [16]. used the same method with chickpeas and saw a significant increase in crop production.

Halo-priming: The process known as "halo-priming" is immersing seeds in solutions of inorganic salts, such as calcium chloride, sodium chloride, potassium chloride, and potassium nitrate. Certain salt solutions have the potential to have both direct and indirect nutritional benefits. The halo-priming approach has been used in several research to increase agricultural production and seed germination in alkaline soil. 27 has assessed how four cultivars of sunflower seeds (*Helianthus annuus* L. cultivars) responded to priming with potassium nitrate and sodium chloride in an alkaline environment, as well as the development of the seedlings. Primed seeds resulted in higher plant germination rates, robust seedlings, and a significant yield of plants per unit area. However, as NaCl salinity rose, there was a drop in the percentage of germination and the emergence of seedlings in both treated and untreated seeds; however, the decline was less pronounced in primed seeds.

Osmo-priming: Instead of soaking seeds in pure water, osmopriming entails soaking them in an osmotic solution with low water potential for a predetermined amount of time, then letting them air dry before planting. Osmotic solutions' low water potential causes water to enter seeds slowly, preventing radicle protrusion but allowing for progressive seed imbibition and early germination stages to be activated [17]. Priming agent water potential typically ranges from -1.0 to -2.0. Nonetheless, water potential values and priming treatment duration should always be tailored to the species, cultivar, and occasionally seed lot. Polyethylene glycol (PEG), mannitol, sorbitol, glycerol, and inorganic salts including NaCl, KCl, KNO_3, K_3PO4, KH_2PO_4, $MgSO_4$, and $CaCl_2$ are among the several substances employed in the osmopriming process [18].

Many osmotic priming agents are utilized, with polyethylene glycol (PEG) being the most often employed. Other osmotic priming agents include sugar, glycerol, mannitol, sorbitol, and specific vermiculite compounds.

Osmo-hardening: Osmo-hardening is soaking seeds in tap water for a whole day, letting them dry again, and then hardening them with solutions containing KCl and $CaCl_2$. Osmohardening, hydro-priming, and on-farm priming were the three priming treatments used in a research conducted by [1] to evaluate the impact on direct seeded rice. Osmohardening with $CaCl_2$ was the most effective of all three treatments, and it was followed by KCl. Increased growth, a large number of tillers, longer and more productive kernels, and higher concentrations of K, P, and Ca all contributed to the rise in crop output, whereas unproductive kernels and undesired, inefficient spikelets decreased.

Hormonal priming: The term "hormonal priming" describes the application of hormones to seeds, such as GA_3, salicylic acid, ascorbate, kinetin, jasmonic acid, etc., to aid in the growth of seedlings. A shown the effects of gibberellic acid priming on the growth and metabolic parameters of the chickpea DCP 92-3 cultivar. After 90 and 100 days after planting, chickpea seeds primed with four different concentrations of GA3 shown a notable increase. The highest effects were achieved when the seeds were soaked for eight hours at a concentration of 10-6 M. Additionally improved were the growth metrics (seed yield and leaf area/plant, pod number and shoot length) and biochemical (protein content, carbonic anhydrase (CA) activity). Gibberellins are known to control physiological and developmental processes in a variety of plants, including germination, stem and leaf growth, food production, transportation, and partitioning. They also stimulate the transcription of the mRNA for hydrolytic enzymes in these plants.CA improves nutrient absorption and membrane permeability. Gibberellic acid, IAA, lipase activity, proline and soluble sugars, POD, and CAT activity concentrations were also higher, and these substances are important in promoting plant development. Large cationic polysaccharide chitosan functions as a biostimulator, promoting physiological, biochemical, and molecular aspects of several essential plant functions. This implies that under low temperature stress, chitosan may accelerate seedling germination and development. The findings indicated that seed priming of salicylic acid (SA) @ 200 ppm and scaling up of potassium nitrate (KNO3) up to 1.5% as foliar application significantly enhanced the yield (grain yield, stover yield and biomass yield) and economics, nutrient uptake and quality of lentill [19].

Matrix priming: The term "matrix priming" describes the practice of limited water usage seed incubation in a solid, non-soluble matrix or polymer. Matrix examples include vermiculite, sand, and so forth. In an experiment by, sand matrix increased germination characteristics by up to 50%, but carrot seeds responded better to the hydropriming approach [20]. Four approaches were used in this experiment: hydro, sand matrix priming, halo, and osmopriming. Sand matrix priming included combining sand and water to obtain a certain amount of water holding capacity.

Nutripriming: By enhancing the nutritional content of the seeds, nutripriming entails priming the seeds in a nutrient solution to increase seed quality. Because they enable two essential plant functions, photosynthesis and respiration, which when limited can reduce overall growth and grain output, micronutrients are critical to plant growth (Fercha et al., 2014). Micronutrients can be used in three different ways to address this issue: directly onto seeds, as a spray on leaves or plants, or applied to the soil. Since fewer micronutrients are required, seed treatment has been shown to be a superior choice among them for enhancing seedling development and grain output [21]. conducted an experiment on dill (*Anethum graveolens*) to assess the effects of iron and boron seed priming separately and in combination. He experimented with a range of concentrations (0.5 to 2%, with a variation of 0.5%) both singly and in combination (1.5% iron plus 1% boron). He discovered that priming seeds with 1.5% iron plus 1% boron resulted in a significant increase in the percentage of germination, seed and essential oil yield, and seedling vigour index; however, the index of seedling vigour was limited when iron concentration was increased beyond 1.5% and boron concentrations beyond 1%. Micronutrient priming speeds up the pace at which seeds absorb water and promotes its use in various metabolic processes.

Bio-priming: It is the process of treating seeds with advantageous microorganisms while maintaining regulated moisture levels, a technique known as "bio-priming" improves the germination process without causing the radicle to emerge. It is linked to altered internal plant hormone levels (Li et al., 2012), increased hydrolytic enzyme activities (28;29), reactive oxygen species (ROS) detoxifying enzyme activities (Jeevan et al., 2015), and differential gene expression in plants that contributes to enhanced plant growth and resistance against biotic and abiotic stress. Novel investigations at the transcriptome, proteome, and biochemistry levels are required to comprehend the function of biopriming with PGPRs in phyto-stimulation and nutritional improvement.

Nano priming: A novel technique for seed priming, known as "nano priming," uses nanoparticles (NPs) such as zinc oxide, iron oxide, titanium dioxide, silver nanoparticles, etc. Applied fertilizers or nutrients are not used by plants because they are washed away or degraded by light and water. The delivery of nutrients to plants through nanoparticulate material allows for the adequate and restricted use of macromolecules and nutrients at a specific site, which is necessary to enhance plant growth [22]. A laboratory study was conducted by [23] to ascertain the stimulatory or inhibitory effects of nano-sized Ag, Cu, and Fe on wheat. The results showed that iron was more stimulating for root-shoot length and germination percentage, while copper had an inhibitory effect on growth, suggesting that iron was stimulatory and copper was inhibitory.

Biochemical markers such proteins, carbohydrates, chlorophyll, and reducing sugars were higher in primed seeds than in control seeds. Similarly, employing anatase nanoparticles (TiO_2) to study the germination of pepper (*Capsicum annum* L.) seeds. It's possible that this improved nitrogen metabolism and photosynthesis, which in turn improved seedling development. Increased pigment and chlorophyll content due to enhanced electron transport, photosynthetic efficiency and ribulose-1, 5-bisphosphate carboxylase/oxygenase activity resulting in carbohydrate synthesis, and electron transport chain. This could have improved nitrogen metabolism and photosynthesis and ultimately improving seedling growth. However, larger concentrations suppressed germination, most likely as a result of increased NP absorption and accumulation inside the cells, which reduced cell division and elongation and inhibited the hydrolytic enzymes needed for food mobilization during the germination process. investigated the biological effects of NPs on root elongation and seed germination using lettuce, cucumber, and radish seeds [18]. He discovered that all three of the seeds were negatively impacted by CuO and NiO. While TiO2, Fe_2O_3, and Co_3O_4 had negligible phytotoxic effects, Co_3O_4 increased the radish seedlings' root elongation.

Magnetopriming: Plants and other living things have been proven to be significantly impacted by magnetic fields. The surroundings naturally contains the earth's magnetic field, which has a strength of 50 mT [24]. The unit of measurement for magnetic flux density is Tesla (T), which is equivalent to kgs-2A-1, where A stands for ampere. For seed priming, agriculture uses both static magnetic fields (SMF) produced by permanent magnets, such as the earth's magnetic field, or by industrial operations, and electromagnetic fields (EMF) produced by electrically charged items [25].

In order to mitigate the negative impacts of numerous environmental challenges, such as drought, salt, disease, and pests, during germination and early crop growth, magnetopriming is frequently utilized as an efficient pre sowing therapy [26].

The seeds are subjected to a magnetic field, a non-invasive physical stimulant, for a predetermined amount of time during the magnetopriming procedure in order to promote physiological modifications to the seed. In contrast to traditional seed priming, which includes soaking seeds in priming solutions, magnet priming involves exposing the dry seeds to a magnetic field in order to increase crop output, germination, seedling vigor, and stress tolerance [27].

It was discovered that H_2O_2signalling is essential to the process of magnetopriming seeds [28]. In several ways, balanced H_2O_2 functions as a signaling hub for the control of seedling vigor. It is generally recognized that the antagonistic interaction between GA3 and ABA is crucial for both seed germination and dormancy.

As ABA catabolism and GA_3 biosynthesis are simultaneously activated, H_2O_2 plays a well-known role as a signaling hub for the control of dormancy and germination [29]. Increased levels of hydrogen peroxide found in faster germinating magneto-primed seeds, under both water shortage and salinity stress, has been attributed for its role in oxidative signalling during seed germination process. Higher activities of hydrolysing enzymes may be the cause of the improved germination, seedling vigor, and rooting features of seeds treated with SMFs [29]. Nevertheless, little is known about how plants sense metal fields (MFs) and how the signal transduction pathway is regulated. According to Anup et al. [21] blue light photoreceptors/cryptochromes are thought to facilitate MF-perception/signaling in plants. Fig. 1 shows the steps involved in magnetopriming, a potential mechanism of action, and the morpho-physiological impacts on plants.

Main limitations of priming techniques: One method that has shown to be successful in boosting seed vigor is seed priming. Depending on the species, cultivar, and seed lot, different treatments are best. This unpredictability is a significant drawback of the priming approach since it necessitates several attempts to determine the best course of action in each circumstance. Regarding seed priming techniques, there is no "general rule" and no discernible pattern of priming response based on the species' taxonomic standing. This definitely restricts the use of priming therapies in the commercial setting.

Certain priming techniques may suggest a danger of bacterial and fungal medium contamination, which might seriously hinder the germination of subsequently planted seeds.

Priming's main disadvantage is that it shortens primed seeds' shelf life when compared to unprimed seeds As a result, primed seed material has less storability, which raises the expense of material upkeep for growers and seed firms. However, it seems that the loss of viability varies greatly among species, cultivars, and seed batches. Under severe circumstances, priming-induced benefits may even vanish after just 14 days of storage, at which point the seedling produced may outperform seedlings derived from unprimed seeds. However, one of the research' weaknesses is that they frequently use artificially aged seeds in their trials, which may not be entirely relevant from a genuine aging process because of the short-term high temperature exposure in a wet environment. Some studies, using classical long-term strategies, reported that longevity is not necessarily affected or may even be increased by priming treatments.

When kept at medium temperature, oxygen did not cause primed seeds to re-establish a genuine quiescent state following dehydration, but at low temperatures, oxygen had no effect. Oxygen during storage may initiate metabolic activities in primed seeds.

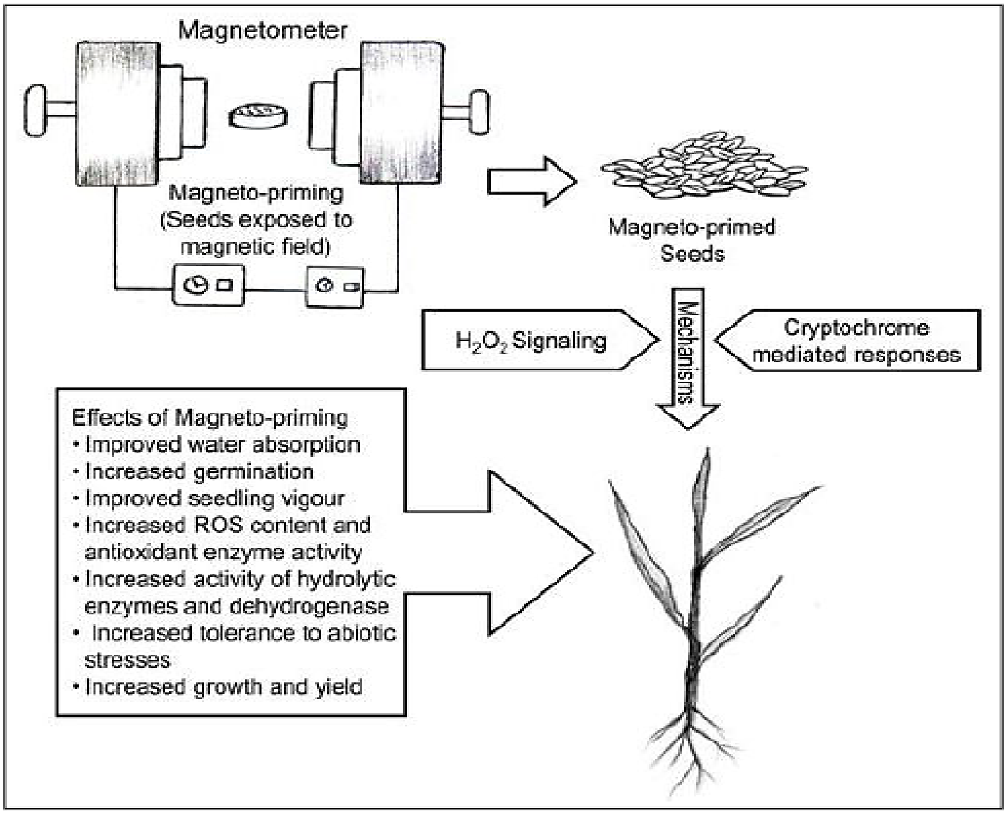

Fig. 1. Magnetopriming: process, possible mechanism of action and morphophysiological effects on plant

Repeated priming treatments following storage have the potential to somewhat mitigate the detrimental impact on seed viability in certain circumstances, but in other circumstances, the loss is irreversible and permanent. In any case, the possibility that a second treatment is needed to recover the entire germination potential adds to the expense and unpredictability.

4. CONCLUSIONS

To enhance the germination processes of cultivated plant species, seed companies have been using seed priming, an ancient empirical technique, for decades. Farmers have been doing it for generations. For a very long period, the fundamental processes responsible for this beneficial effect of pre-sowing therapies were unknown. The goal of the current study was to compile the most recent data made available by different instruments that enable the identification of chemical markers conditioning priming efficiency. There are already data available derived from molecular methods applied to a few well-known plant species (rice, rapeseed, tomato, etc.). Now, the function of genes linked to metabolic and cell cycle events is beginning to be understood. These genes mostly encode for translational components such transcription factors, ribosomal subunits, translational initiation factor, enzymes involved in carbon metabolism, and histones. It's important to take into account a potential epigenetic foundation for priming effects. While some investigators observed several alterations in the seed storage protein, others found variations in enzyme activity in response to priming. Additionally, priming has been shown to upregulate cell cycle-related proteins such α- and δ-DNA polymerase.

It is anticipated that protective proteins such as HSP or dehydrins would take on protective roles during the dehydration phase. Comparably, priming may control some proteins that are involved in cell division, water transport, cell wall modification, and cytoskeletal architecture. Tissue preservation during the dehydration stage and water fluxes during the final germination phase may be primarily regulated by gene expression and enzyme activities involved in osmocompatible solute production. The lag period of imbibition appears to be decreasing, according on measurements of water uptake by primed seeds. Aquaporins may be involved in controlling water intake and the following cell-to-cell transfer that occurs during germination; hence, one specific target of the priming treatment is the expression of the related genes. Among the different hypothesis proposed to explain the biochemical basis for germination improvement, DNA replication, cell cycle progression during priming therapy, and cell cycle synchronization during the G2 phase. Both the priming treatment and the post-germinative stages include DNA synthesis. The rearrangement of mitochondrial integrity and the alteration of the membrane structure are also observable changes. The enhanced behavior of plant material may also be explained by the priming treatment's activation of antioxidative qualities, particularly when final germination and/or growth take place under stressful conditions. One significant obstacle to seed businesses using the priming approach is the reduction in storage capacity caused by priming. Primed seeds can last longer if they are partially vacuum-sealed. Increased antioxidative activity that reduces the buildup of total peroxide during long-term storage may be linked to longer lifespans. Finding the right treatments to revitalize old, dry seed lots and raise their mean percentage of germination to levels adequate for commercial use is another difficulty for private seed companies. Although it's possible that genetics has a role in priming treatment response, there are currently no data addressing this significant issue to our knowledge. Therefore, more research is required to determine not only the genes that priming regulates, but also the genes that may affect priming response and efficiency.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of this manuscript.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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