



***Role of Seed Priming in Enhancing Germination under  
Abiotic Stresses (Drought, Salinity, Heat)***

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**Abstract:** *Seed germination is a critical stage in a plant's life cycle and is highly vulnerable to abiotic stresses such as drought, salinity, and high temperature, which can severely impair physiological and biochemical processes. Seed priming a controlled pre-sowing hydration treatment has emerged as an effective strategy to improve seed performance under these unfavorable conditions. This review highlights the mechanisms and benefits of different priming techniques, including hydropriming, Osmo priming, hormonal priming, bio-priming, and nano-priming, in mitigating abiotic stress impacts. Primed seeds exhibit enhanced enzymatic activity, antioxidant defense, osmotic regulation, and hormonal balance, resulting in improved germination, seedling vigor, and stress resilience. Under drought conditions, priming promotes osmotic adjustment and antioxidant capacity; under salinity stress, it maintains ion homeostasis and photosynthetic efficiency; and under heat stress, it stabilizes proteins and activates heat shock responses. Recent advancements such as molecular, nano-, and bio-priming demonstrate the potential to enhance crop tolerance and productivity sustainably. Overall, seed priming represents a cost-effective, eco-friendly, and practical approach to strengthen crop resilience and ensure food security under changing climatic conditions.*

**Keywords:** *Seed priming, Germination enhancement, Abiotic stress, Drought stress, Salinity stress, Hormonal priming, Nano-priming, Bio-priming, Antioxidant defense, Osmotic adjustment, Stress physiology, Sustainable agriculture climate-resilient crops*

## **1. Introduction**

Seed germination is an important phase of the plant life cycle and is responsible for seedling establishment under abiotic stresses such as drought, salinity, and temperature extremes. This is when the seed turns into a growing plant from being in a dormant state, it is sensitive to

environmental factors (Bentsink and Koornneef, 2008). Under abiotic stress conditions, seeds have difficulty in germinating due to the disruption of physiological and biochemical processes involved in this conversion. For example, salinity can interfere with water absorption – leading to osmotic stress and extreme temperature may cause protein denaturation or a breakdown of important metabolic processes for germination (Qi et al., 2023).

Plants are expected to manage these stressors during the transition of seeds germinating into seedlings. It is this stage at which seeds must combine numerous endogenous and exogenous cues to turn on the appropriate adaptive responses (Carrera-Castaño et al., 2020; Jan et al., 2025). Hormones, especially phytohormone such as abscisic acid (ABA) are involved in seed germination under some types of abiotic stress. It is well studied that ABA molecule works by modulating stress tolerance related genes in order to coordinate that germination only occurs when the environment is favorable (Rehman et al., 2022; Nambara et al., 2010). Melatonin, a plant modulator, has been known to play a crucial role in promoting seed germination under stress. It enhances the germination by maintaining ionic balance, hydrolyzing storage proteins under salinity stress, and regulating starch metabolism under heat treatment (Wang et al., 2024). Furthermore, practices such as seed priming (soaking seeds before planting) can also induce physiological/biochemical transformations enhancing germination velocity and resistance to stress (Jisha et al., 2013; Jan et al., 2025). Seed priming techniques via osmopriming, using agents such as polyethylene glycol (PEG), may precondition seeds for fast germination and vigorous seedlings establishment even under adverse environments (Jatana et al., 2024; Lei et al., 2021). An efficient germination of seeds under abiotic stresses would enable plants to get ahead competitively, establishing deeper roots and better subsequent fitness throughout the plant life. Such plasticity is essential to maintain crop yield, and also to support vegetation in stressful environments beneficial from aspects of food security and ecosystem restoration (Daszkowska-Golec, 2011; Zhang et al., 2023).

The abiotic stress of drought, salinity, and high temperatures are the major constraints to seed germination. These stresses affect the germination processes at different levels, which in turn lead to plant growth/development outcomes. Drought stress, which is associated with water limitation, influences germination by reducing water potential and impairing the ability of seeds to take up water. This results in metabolic dysfunction and diminished enzymatic activities required for the

mobilization of seed reserves (Rangani and Parikh, 2017; Jan et al., 2025). When under water stress, the seeds are subject to osmotic pressure resulting in lower germination and slower rate of germination. For example, simulated drought stress by polyethylene glycol application remarkably reduces seed germination and also the enzymatic activity involved in seed reserves utilization (Atta et al., 2020; Sidari et al., 2008; Jan et al., 2025). Furthermore, Introduction of ion toxicity and osmotic stress caused by salinity stress reduces water potential accretion and generates a Kaleidoscope of ions imbalance in the seeds (Munns and Tester, 2008). Salt stress also induces a decrease in the content of germination stimulants, e.g., gibberellins (GAs), and an increase in abscisic acid (ABA) levels that prevent germination. Salinity alone exerts a greater inhibitory effect at high salt concentration and increased temperature, though some plant species exhibits salinity tolerance at the time of germination (Gupta and Huang, 2014). Additionally, salinity is also reported to be favorable for seed germination of species like *Melilotus officinalis* at 90 mM and above, though this tolerance level is not the same in all varieties (>per 90 encourages), phenotypes (Ghaderi-Far et al., 2010; Lin et al., 2015).

In additions, Excessive high temperature during heat stress could have an adverse effect on germination through disorganization of membrane system and suppression of enzymes serving as a trigger for seedling growth (Los and Murata, 2004). Seeds have an optimum species-specific temperature for germination and deviations from this range (particularly above the estimated maximum) is expected to result in lowered germination rates, coupled to increases or decreases on enzyme activity which participates in seed metabolism (Tamura et al., 2006). For *Pinus pinea*, seeds germination rate decreases with temperatures above this optimal range (Sidari et al., 2008). Affects by the dues and lethallness of those stress factor influences on seed germination. Strategies such as genetic modification and seed priming with agents like PEG or water-soluble nanoparticles can, in case of a number of species, decrease the negative influence by improving stress tolerance at germination (Basu et al., 2017; El Moukhtari et al., 2022). Effective management strategies under such stress conditions would be necessary to enhance seed germination and plant development in the field under stressful environmental conditions.

Seed priming has been developed as a potential strategy to improve crop tolerance against biotic and abiotic stresses. The method comprises of priming of seeds with different agents inducing physiological and biochemical reactions without producing radicle emergence (Paparella et al.,

2015; Jan et al., 2025). Many priming techniques including hydropriming, osmopriming, biopriming and hormonal priming provide environmentally safe-low-cost options for enhancing seed germination, vigour and stress tolerance in crops (Jatana et al., 2024; Jisha et al., 2013). The power of seed priming is that it can trigger the molecular and physiological processes inside the seeds, leading to increased rates of germination and plant growth, even in unfavorable situations like drought, salinity, heat, and cold stress (Aswathi et al., 2021; Jatana et al., 2024). For example, seed priming can increase root hair density and length under drought, promoting water absorption (Chen et al., 2023). This response primes the plant to better respond to subsequent stresses by activating stress-related genes and pathways, such as plant hormone signal transduction and MAPK signaling (Chen et al., 2023).

Additionally, seed priming has the benefit of cross-tolerance to other stress factors and adaptation for environmental hazards in parent plants which will ameliorate the next generation's tolerance capacity (Jatana et al., 2024; Jan et al., 2025). Many researches have reported its efficacy in enhancing the seeds capacity to withstand multiple stresses simultaneously, and promoting post-stress recovery by stimulating osmolyte accumulation and antioxidant activities (Aswathi et al., 2021; Parera and Cantliffe, 1994). Research has also shown that the seed priming with nanomaterials leads to enhanced uptake and efficiency of priming agent as compared to the bulk chemicals. This is attributed to the better physicochemical properties of nanomaterials that facilitate improved cellular level interaction and minimize the detrimental effects of abiotic stressors such as drought and high salinity (M S et al., 2021). Further, approaches like bio-priming incorporate microbial products contributing towards abatement of stress by improving the seed efficiency and reducing the usage of chemicals (Rajendra Prasad et al., 2016).

The adoption of phytohormones and growth regulators in seed priming is identified as a crucial research strategy to ameliorate negative abiotic stress impacts through promotion of growth potential and yield performance under stress. This strategy enables plants to more quickly and efficiently response to stress (Rhaman et al., 2020). Seed priming is regarded as a breakthrough in agriculture that leads to enhanced crop tolerance and productivity under the challenges of global climate change (Jarrar et al., 2024).

## **2. Concept of Seed Priming**

Seed priming, a pre-sowing seed treatment method to improve germination and seedling growth by controlled hydration. The process includes soaking of the seeds in a priming solution at certain environmental conditions and subsequent drying to stimulate pre-germinative metabolic activities but not allowing seeds for complete germination (Jisha et al., 2013; Jatana et al., 2024; M. A. Khan et al., 2024; Raj & Raj, 2019). Seed priming is known to involve partial activation of seed germination triggering metabolic pathways. This in turn leads to a series of biochemical and physiological cascades, including an increase in enzyme activity (such as  $\alpha$ -amylase), induction of antioxidant responses, and reinforcement of stress responses (Hussain et al., 2015; Paparella et al., 2015; Jan et al., 2025). Following these alterations, the germination synchrony is enhanced and faster as well as better seedling vigor is resulted, leading to efficient nutrient uptake coupled with increased stress resistance tolerance to biotic and abiotic factors (Jatana et al., 2024; Srivastava et al., 2021).

The advantages of seed priming include improving seed vigor, uniform emergence of seedlings, better yield, and greater sustainability in agriculture. Seed priming could also contribute to enhancing the stress memory of plants, with future stresses being more easily counteracted (Conrath et al., 2015; Afzal, 2023; Srivastava et al., 2021). Seed priming is beneficial, albeit species and environment dependent, thus needs to be tailored for different crops and conditions. This method has enormous potential to improve agricultural productivity and sustainability, with additional studies necessary for diversification across species and ecological conditions (Paparella et al., 2015; Raj & Raj 2019). The priming of seeds is a pre-sowing method that can increase germination, seedling growth, and stress tolerance in plants. Among the different agents and conditions, many techniques of seed priming are used. Here are some of the most notable approaches:

**Hydropriming:** The simplest seed priming that does not involve chemical agents. Seeds are soaked in water for a predetermined duration to initiate metabolic reactions without allowing radicle protrusion. It is employed commonly for its low cost and simplicity (Farooq et al., 2019; Farooq et al., 2006; Jatana et al., 2024).

**Osmopriming:** It is a method of seed soaking in a solution having osmotic potential to regulate the water imbibition. Typical osmotic agents comprise polyethylene glycol and salt solutions.

Osmopriming facilitates even germination and increases seedling growth by promoting metabolic activities at certain hydration levels (Capron et al., 2000; Farooq et al., 2019).

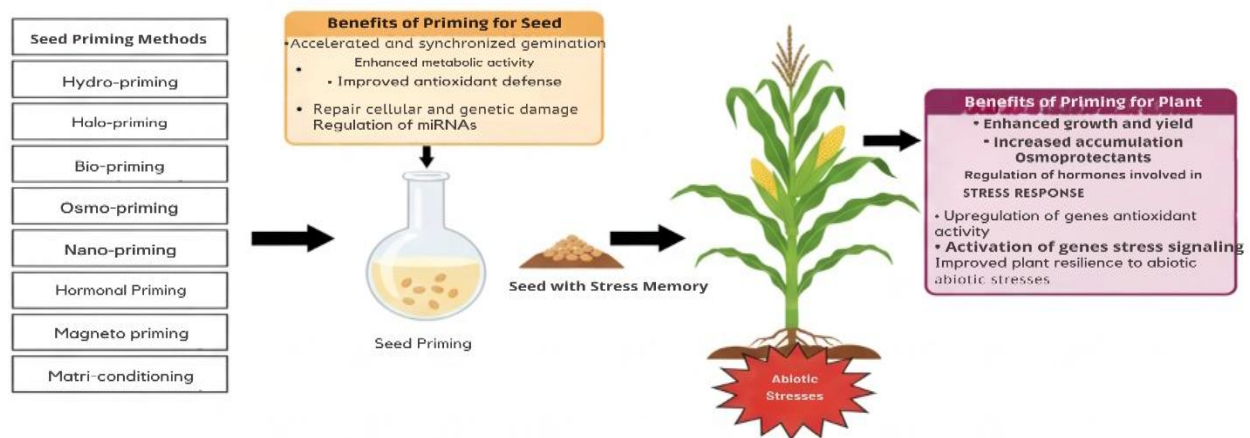
**Hormonal priming:** Known as hormoprimering too, this method involves allowing seeds to presoak in a solution with plant growth regulators or hormones like salicylic acid (SA) and gibberellic acid. Hormone priming has a significant effect in increasing stress tolerance and early seedling growth by regulating the hormone network and mechanisms in seeds (Rehman et al., 2011; Farooq et al., 2019; Tamindžić et al., 2020).

**Nano-priming:** This new technology is the application of nanoparticles (NPs) for improving seed priming. Nano-priming has been reported to induce NPK uptake, enhance water uptake by increasing the expression of aquaporins, and stimulate enzymatic and antioxidant responses (Nile et al., 2022; Khodakovskaya et al., 2009; Ruttkay-Nedecky et al., 2022).

**Bio-priming:** This refers to the treatment of seeds with beneficial microbes, including plant growth-promoting bacteria or fungi. Seedling vigor, diseases, and stress tolerance can be improved by the bio-priming process wherein beneficial microbiomes on seed surfaces are enhanced (Jatana et al., 2024).

**Nutripriming:** This involves soaking seeds in solutions containing essential nutrients or minerals, such as zinc or potassium nitrate that can promote nutrient uptake and help with better plant growth and yield. Frequently, the nutrient-use efficiency of primed plants is enhanced (Nadeem et al., 2020; Macdonald & Mohan, 2025).

**Halopriming and Solid Matrix Priming (SMP):** **Halopriming** refers to seed imbibition in solutions containing salts that activate endogenous mechanisms for salt tolerance, whereas Solid Matrix Priming (SMP) needs the use of a solid body system (vermiculite, clay, or paper) saturated with water or nutrient solution to imbibe seeds and promote physiological and biochemical activities during germination (Lutts et al., 2016; Farooq et al., 2019; Raj & Raj, 2019).



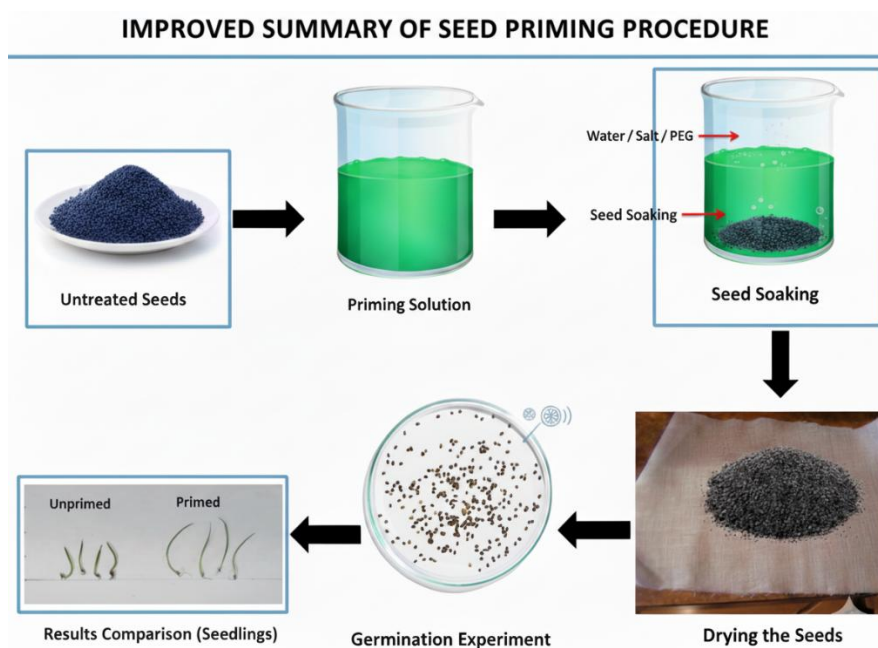
**Fig.1. Different Seed Priming Methods.**

All the three approaches exploit various agents to prime seeds against the attacks of environmental stress, improve germination characteristics and optimize plant nosglobl development capacity, and yield potential (M. A. Khan et al., 2024; Macdonald & Mohan, 2025). Seed priming is the controlled hydration to first limits of seed uptake, which in turn increases the osmotic potential (Wang et al., 1995), and as a result leading to improvement in bio-chemical and physiological characteristics of seeds that ultimately contribute to increased germination and stress tolerant capability. Upon priming, seeds experience many critical physiological events including cell cycle control, ultrastructural variation in seed structure and oxidative stress response. These mechanisms contribute to synchronizing germination and enhancing the uniformity of seedling emergence (Raj & Raj, 2019).

Biochemically, seed priming induces a series of metabolic processes such as those associated with enzyme activation and protein synthesis that are involved in earlier and more uniform germination. Furthermore, commencement of antioxidant defense system and repairing of the cellular elements including DNA play critical roles in biochemistry of seed priming. This increases the vigor of seed and tolerance for variety of stressors (Waqas et al., 2019).

Seed priming methods may induce enzymatic, hormonal and molecular changes in the seed which are responsible for increased tolerance to biotic as well as abiotic stresses. These stress responses may be associated with the proteomic and metabolomic changes that would further a stronger plant, which is able to tolerate environmental downside (Jatana et al., 2024). Collectively, seed priming not only promotes germination and covert resistance to suppress etiolation the growth if future beneficial microbes are present and under induce equipped condition (Figure 2), rather it encourages a series of physiological and biochemical changes enhancing overall plant growth as well as yield (Bose et al., 2018; Jan et al., 2025) thus becoming an important strategy for sustainable agriculture including cropshurst response phytohormones mediated signaling pathways affecting crop production.

**Figure. 2 Seed priming procedure**



### 3. Seed Priming under Drought Stress

Drought stress has a profound impact on seed germination and early seedling growth through the reduction of germination parameters, and modification of physiological properties. Under drought over plant species (Faraji & Sepehri, 2019;) and germination of percentage are significantly reduced, as well as germination rate, seedling vigor index are also decreased by reduced root length and shoot length (Tak et al., 2018;). The mechanism is mainly attributed to osmotic stress caused

by an inadequate water supply, which affects water absorption leading to germination and seedling growth. Over recent decades, PEG has been widely used to simulate drought stress in laboratory studies of plant species such as wheat, the germination percentage, germination energy, growth rates and seedling vigor of wheat are all significantly decreased by PEG-induced drought stress compared with control samples (Faraji & Sepehri, 2019). Likewise in maize and sorghum, as osmotic potential increases, numbers of germinated seeds, root and shoot growth and seedling vigor indices decrease, with maize more sensitive to drought stress than sorghum (Queiroz et al., 2019; Jan et al., 2025). In addition, about the germination traits of Chinese cabbage seeds, with drought stress increasing their number decreases, however seed priming mitigates some negative effects (M. Yan 2015).

Drought alters important biochemical and physiological processes as well. For example, it promotes the accumulation of abscisic acid (ABA) and reactive oxygen species (ROS), both repressors for seed germination. ABA accumulation suppresses the seed germination, and elevated ROS level and decreased activities of antioxidants including superoxide dismutase (SOD) and catalase (CAT) etc., aggravate the damages on seedling growth (Liu et al., 2019). It has been reported that seed priming provides some relief against deleterious effects of drought stress. Various treatments, such as those involving melatonin priming increase the germination percentage, rate and enhance physiological parameters through manipulation of antioxidant enzyme activity and decrease ROS levels (García-Cánovas et al., 2024; Guo et al., 2022). These findings provide clues to possible approaches for increasing the drought stress tolerance at the key stages of plant development like germination/initial growth.

**Osmotic Adjustment:** There is high osmotic adjustment in primed seeds due to their ability of having control over water uptake and holding. In this process, the role of cell turgor is critical to maintain growth under drought. Pre-sowing seed treatments related to the priming technology, osmopriming with calcium chloride (CaCl<sub>2</sub>) or potassium nitrate (KNO<sub>3</sub>), play a role in maintaining osmotic adjustment and enhancing seed germination and seedling growth even under drought stress (Bismillah Khan et al., 2015; Marthandan et al., 2020).

**Antioxidant Activity:** This seed treatment improves the activity of antioxidant enzymes i.e., superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX). These enzymes are

centrally involved in the response to oxidative stress through decreasing cellular concentrations of ROS and thus protecting cellular structures from damage due to oxidation. The enhanced antioxidant defense system adapted to these primed seeds may be sufficient to mitigate the toxic effects associated with drought-mediated oxidative stress (Ocvirk et al., 2020; M. Yan, 2015).

**Gene Regulation:** Seed priming also affects gene regulation, particularly stress-related pathways and protective proteins such as dehydrins. The use of growth regulators during priming has the potential to induce genes for osmotic and oxidative stress and increase capacity of seed in tolerating condition imposed by drought. For example, DA-6 priming increases the expression levels of some dehydrin proteins-encoding genes crucial for cellular protection under dehydration (Hassan et al., 2021).

**Table 1. Major abiotic stresses affecting seed germination and their physiological effects**

<b>Stress Type</b>	<b>Mechanism of Inhibition</b>	<b>Key Physiological Effects</b>	<b>Reference</b>
<b>Drought</b>	Reduced water potential, osmotic stress	Decreased germination %, reduced enzyme activity	Faraji & Sepehri (2019); Tak et al. (2018); Queiroz et al. (2019)
<b>Salinity</b>	Ion toxicity, osmotic imbalance	Reduced GA, increased ABA; ionic imbalance (Na <sup>+</sup> /K <sup>+</sup> )	Uçarlı (2021); Yadukrishnan et al. (2020); He et al. (2019)
<b>Heat</b>	Protein denaturation, oxidative stress	Reduced vigor, delayed germination	Reed et al. (2022); Liu et al. (2019)

Experimental evidence also suggests that drought-induced priming has benefits in terms of tolerance, especially when bacterial-based primes are involved. One study showed the impact of priming wheat with rhizosphere bacteria isolated from extreme environments. This strategy

resulted in a 78% increment in plant biomass and five times higher survivals to severe drought. The study was based on measuring stress elicited volatile emissions from bacterially primed drought stressed wheat seedlings, showing that bacterial priming can be used to increase the resistance of plants to drought by augmenting water use efficiency and fitness in adverse conditions (Timmusk et al., 2014).

Furthermore, reports are available related to the use of Polyamines (PAs) for enhancing tolerance of plants against abiotic stresses like drought. Polyamines are important small molecules involved in plant stress tolerance. There is evidence that exogenous application or genetic modulation of polyamine levels can confer abiotic stress tolerance in crop plants. For example, polyamines seed priming as a potential strategy to improve drought resistance has been introduced (Alcázar et al., 2020; Jan et al., 2025). Bacterial priming and polyamines applications are also promising strategies with support of experimental data to enhance plant drought tolerance. These approaches are promising solutions to improve agricultural resilience against water shortage and food security under climate change.

#### **4. Seed Priming under Salinity Stress**

Seed germination and seedling establishment are also significantly inhibited by NaCl stress through a variety of strategies. Most essentially, salinity affects plants through osmotic stress, ion toxicity and oxidative stress. Osmotic stress prevents the absorption of water necessary for seed germination, and ion toxicity (in particular by sodium and chloride ions) interferes with cellular homeostasis and may damage cell structures. This combination slowed germination and decreased the rate of emergence, resulting in poor seedling growth rates and inferior stand establishment (Uçarlı, 2021).

Furthermore, salinity may disrupt the hormonal balance essential for germination. It reduces the contents of germination stimulants such as gibberellins (GAs) and increases abscisic acid (ABA) which is responsible for preventing seed germination and inhibiting early growth of the seedling (Uçarlı, 2021). The physiological milieu within the seed is also influenced by alterations in membrane permeability and water kinetics that aggravate the unfavorable effects on germination (Uçarlı, 2021; Yadukrishnan et al., 2020).

Studies have demonstrated that overexpression of certain genes involved in salt stress can promote the germination process under salt stress. For instance, the QTL qSE3 has been associated with enhanced uptake of K<sup>+</sup> and Na<sup>+</sup>, increased ABA biosynthesis and altered ABA signal transduction resulting in improved seed germination and decreased salt-induced inhibition of early-stage growth (He et al., 2019). In order to reduce these risks, priming of seeds has been recommended. Seed priming, whereby seed is treated to provide a level of hydration that improves germination and seedling establishment even under saline conditions. This method helps to prevent the stress and to further prepare the seeds by improving their physiological readiness for germination (Uçarlı, 2021). Several priming tactics have been reported to alleviate the salinity stress in plants, where they put significant physiological and biochemical resilience mechanisms into operation. The efficacy of osmopriming, hormonal priming, and nano-priming in mitigating salinity stress is summarized as follows:

**Osmopriming:** With this method, the seeds are primed with osmotic agents, inducing early germination in order to make the plants more resistant to salinity stress. The accumulation of osmolytes, such as proline and glycine betaine are an important adaptation of cells to maintain cellular osmotic potential due to the increase in pressure. It also increases the levels of antioxidant such as superoxide dismutase, catalase and peroxidase in saline-stressed plants thereby lowering oxidative stress damage (Abdelhamid et al., 2019; Borromeo et al., 2023).

**Hormonal Pretreatment:** Plant growth regulators, or phytohormones, such as gibberellins, cytokinins, and abscisic acid, can improve the plant's response to stress. The above treatments mediate growth and stress response pathways that help maintain membrane integrity (via enhanced enzymatic antioxidant activity) and ionic equilibria when plants are grown in saline substrates. Polyamines such as putrescine, spermidine and spermine have also been applied in hormonal priming for increasing salinity stress tolerance through improving photosynthetic capacity and protecting the cellular structures of the plants (Borromeo et al., 2023).

**Nano-priming:** Although no definite context must be found on nano-priming, it is a general technique that nanoparticles are used as carriers to transfer stress-tolerant molecules or nutrients in the plants. This approach has the potential in increasing nutrient use efficiency, amelioration of

stress tolerance through superior antioxidant response and targeted application that result in enhancing plant defence system against salt stress (Zulfiqar et al., 2022).

Seed priming under salinity condition increases physiological and molecular responses leading to better tolerance and growth. A number of benefits were reported from seed priming with various agents according to the studies: Primed seeds, such as graphene oxide treated ones, have shown greater intolerance to salinity stresses exhibiting a higher percentage of germination with increasing rates of younger seedlings. For example, after the priming of seeds with graphene oxide, germination rates and seedling growth were found to be enhanced under stress conditions (N. Yan et al., 2024). Priming is beneficial in well-maintaining the photosynthetic efficiency and chlorophyll level. For instance, halopriming agents used for priming wheat seedlings enhanced photosynthetic efficiency (Fv/Fm and Ft) when subjected to salinity stress condition (Saddiq et al., 2019). Similarly, priming with spermidine increased photosynthetic pigments in *Brassica napus* (Stassinis et al., 2021). Activity of antioxidant enzymes including superoxide dismutase and catalase has been observed to increase in primed plants, thus protecting them against oxidative damage. Nano-silica priming, for instance, and was found to enhance the antioxidant enzymes activities of maize (Naguib & Abdalla, 2019). Additionally, saponin primed soybean showed enhanced antioxidants metabolism and stress related osmolyte accumulation (Soliman et al., 2020). Priming is able to regulate hormone content and promote the metabolic pathways associated with salinity stress responses. GO-primed peanut seedlings exhibited the regulation of carbon and nitrogen metabolism, photosynthesis, and phytohormone signaling pathways (N. Yan et al., 2024). In olives, hormones signaling and defense crosstalk proved to be essential in primed responses in transcriptomic and proteomic analyses (Skodra et al., 2022). By priming the cell, it optimizes its ion status, as there is a lower rise of sodium ions associated to a higher retention of potassium ions that promote cellular function. The application of TiO<sub>2</sub> NPs in maize increased the membrane stability by lowering sodium leakage and increasing potassium retention (Shah et al., 2020).

**Table 2. Physiological and biochemical responses induced by seed priming**

<b>Parameter</b>	<b>Non-Primed Seed</b>	<b>Primed Seed</b>	<b>Effect of Priming</b>	<b>Reference</b>
<b>Antioxidant enzymes (SOD, CAT, APX)</b>	Low activity	High activity	Detoxification of ROS	Bose et al. (2018); Cao et al. (2019)
<b>Proline content</b>	Low	Elevated	Osmotic adjustment under stress	Hassan et al. (2021); Aswathi et al. (2021)
<b>ABA/GA ratio</b>	High ABA, low GA	Balanced hormone levels	Promotes germination	Rhaman et al. (2020); Rehman et al. (2022)
<b>Membrane stability index</b>	Low	Increased	Maintains cellular integrity	Anjos Neto et al. (2020); Chakraborty & Dwivedi (2021)
<b>Germination percentage (%)</b>	40–60%	80–95%	Improved vigor and uniformity	Afzal (2023); Farooq et al. (2019)

## 5. Seed Priming under Heat Stress

High temperature is a common threat to seed germination and vigour, as it can cause marked changes in seed physiology and metabolism. High temperature during seed development and maturation can reduce seed size, number and fertility leading to delayed germination as well as reduced vigor in a range of crops including cereals, legumes and vegetables. Heat stress can reduce seed germination and increase seed dormancy, especially in cooler-germinating and establishing crop plants (Reed et al., 2022).

Seed priming is now recognized as an efficient approach to enhance heat tolerance at germination stage. This pre-sowing treatment consists of treating the seed with water or a particular solution for a set period and then allowing them to dry, thus improving physiological condition of seeds to germinate. Seed priming induces multiple physiological and biochemical changes, which accelerate and synchronise germination. Priming causes enzymatic, hormonal, physiological, and molecular changes in seeds that lead to increased stress tolerance during germination and seedling emergence (Jatana et al., 2024).

Seed priming with substances such as seaweed extract and CaCl<sub>2</sub> specifically under heat stress enhances germination parameters like percent, speed of germination and seedling vigor. Priming mitigates the production of damaging reactive oxygen species such as hydrogen peroxide which accumulate under heat stress and enhances antioxidant functions. These modifications reduce heat injury to seeds. These mechanisms improve the viability and vigor of seedlings under suboptimal conditions (Anjos Neto et al., 2020; Tamindžić et al., 2023). Stress memory is also activated by seed priming. This process enables seeds to be more resistant to subsequent stresses because of the physiological and biochemical modifications that occur during priming. These changes incorporate an increase in proline, the content of soluble sugars and protein that assist to provide resistance under stress tolerance (Jatana et al., 2024; R. Wang et al., 2024).

Heat shock proteins, antioxidants and hormonal regulation are important in mediating increased performance of primed seeds, especially under stress conditions such as heat and water deficit. Heat Shock Proteins (HSPs): They are essential for stabilizing the structure of proteins in the cells and prevent them from getting denatured, being a very integral part for maintaining resistance to abiotic stress. The end of seed priming could be characterized with, increase in HSPs protein content and its activities, assisted the plant against heat stress. This response is highly important at early germination and seedling stages when environmental temperatures could exceed optimum (Chakraborty & Dwivedi, 2021).

Antioxidants: Antioxidative systems that contain enzymes such as SOD, POD and CAT have an important function in sequestration of reactive oxygen species (ROS) under stress. It has been demonstrated that seed priming increases the activities of these antioxidants, leading to a decrease in oxidation of cellular components. For instance, during seed priming with substances such as

protein hydrolysate or melatonin, there is stimulation of enzymatic and non-enzymatic antioxidants activation that helps in protecting cellular integrity during stress by reduction of hydrogen peroxide and malondialdehyde contents (Cao et al., 2019; W. Wang et al., 2022).

Hormones: Abscisic acid (ABA), gibberellins (GA) and salicylic acid (SA) are phytohormones that play important roles in the response of plants to abiotic, including heat stress. There are reports that seed priming may modify hormonal levels, then affected stress responses and germination and growth highlights. For example seeds that have been primed typically exhibit enhanced germination and growth-related characteristics under stress conditions as a result of alterations in hormone activity. For example, gibberellins stimulate  $\alpha$ -amylase activity for starch hydrolysis that is important under chilling stress for seedling vigor (Ahammed et al., 2016; Nie et al., 2022).

Heat shock proteins protect and stabilize proteins and enzyme system during heat stress, antioxidants counteract oxidative stress by scavenging free radicals, hormones control growth and stress response in primed seeds which makes them better tolerant under adverse conditions.

## **6. Comparative Insights**

The efficiency of seed priming becomes quite variable under various abiotic stress conditions like drought, salinity and heat stresses. Seed priming is a pre-sowing technique which increases the seed germination and growth performance by subjecting seeds to certain stimuli, stimulating metabolic pathway the result in plants with stress tolerance.

Seed priming has also been reported to improve drought resistance. For example, chemo-priming with compounds such as mannose, mannitol and hydrogen peroxide have been demonstrated to alleviate the damage caused by drought stress in wheat. In particular, mannitol elevated the seedling fresh weights, root + shoot FW under non-stress conditions whereas hydrogen peroxide increased root length and DW during drought (Hameed & Iqbal, 2014). In a similar line, melatonin-priming enhanced the root hydraulic conductivity and controlled the enzymes involved in antioxidant defence of wheat plants under combined drought and salinity stress (Fu et al., 2024). Also, it was reported that an increase in germination of Chinese cabbage under different levels of drought stress by potassium nitrate and urea as priming agents (M. Yan, 2015). In salinity stress, gibberellic acid seed priming was found successful in improving the saline tolerance in pea plants

by activating antioxidant systems and controlling ion homeostasis (Ahmad et al., 2020). This treatment also alleviates the salinity-induced oxidative stress and ion imbalances. There do not appear to be any concrete examples of seed priming for heat stress in the literature we were able to access, but it is likely that reactions to heat stress might also benefit from these possible changes due by seed priming such as improved antioxidant systems and increased osmotic adjustment as also reported for both drought and salinity.

## **7. Efficient Priming Methods:**

**Chemo-priming:** Mannitol, mannose and hydrogen peroxide are effective under drought stress through enhancement of seedling vigor and water contents (Hameed & Iqbal, 2014).

**Melatonin Priming:** Effective in mitigating combined drought and salinity stress, increased root hydraulic conductivity, altered antioxidant enzyme activities (Fu et al., 2024).

**Gibberellic Acid Priming:** An effective approach to mitigate high salinity stress by improving antioxidant systems and ions homeostasis in pea seedlings An effectual approach to alleviate high salinity stress via reprogramming of ROS metabolism, ion uptake and transport of PEG primed wheat seeds upholds regulation through tissue water content (Khatoon et al., 2018; Ahmad et al., 2020).

**Osmopriming (PEG):** Provides drought tolerance, enhances germination per cent and antioxidant enzyme activities (Lei et al., 2021; Rhaman et al., 2020).

Various priming treatments are successful under particular stress situations. Chemo-priming, melatonin priming/gibberellic acid (GA3) included priming/ Osmopriming have also shown potential for alleviating drought and salinity stresses in plants; however, their efficiency may highly depend on plant concern as well as intensity of stress.

Seed priming can actually be incorporated into sustainable crop production practices, as they provide several advantages improving agricultural productivity and also preservation of the environment. Seed priming, as a pre-sowing treatment, has known to improve seed germination and seedling growth, which eventually leads toward improved stress tolerance and crop yield (M.

A. Khan et al., 2024). This technique is being considered as an eco-friendly method of farming, which can reduce dependence on the chemical fertilizers and pesticides by improving the natural plant tolerance ability and strength (Chatterjee et al., 2018).

Various types of seed priming including osmotic, hydro, hormonal, microbial and nano-priming have portrayed a potential role in sustainable agriculture. For example, nano-priming strategies use the advances of nanoscale science and technology to enhance plant growth and stress tolerance as well as the nutritional quality from germination to a plants life. This may reduce the necessity for chemical applications in agriculture and help to promote more sustainable farming (Do Espirito Santo Pereira et al., 2021).

Furthermore, seed priming with non-ionizing physical agents (e.g., magnetic field, ultrasonic wave) has emerged as an environmental-friendly practice with positive effect on crop productivity and no damaging impact to the environment (Bera et al., 2021). Homologously, incorporation of ionizing radiation (X and gamma rays) in priming offers an alternative prospect to the conventional chemical seed treatments. Such methods, which need to be further developed for optimization, are less time-consuming with a higher efficiency and provide clean processes (J. Wang et al., 2022).

Chemical seed priming interventions, specifically salicylic acid and gibberellic acid application have been investigated to provide plants with improved tolerance to stress as well as potential epigenetic advantages, reinforcing the concept of sustainable farming practices that are efficient over generations (Macdonald & Mohan, 2025). In addition, PBs used for seed the priming conforms to circular economy senses by exploiting natural bioactive chemicals for improving seed quality and maintaining production sustainability (Wazeer et al., 2024). The transfer of seed priming to sustainable agricultural practices is a multi-dimensional task and continued work will contribute to the improvement in such methodologies maximizing benefits in multiple farming conditions, thus ultimately contributing to increase on-farm sustainability, resilience, and productivity in an environmentally friendly form.

## **8. Challenges and Future Prospects**

Although seed priming is a potential tool to improve seed germination and crop yield, there are multiple constraints for its application in the field. These may limit and prevent its widespread

deployment and effectiveness in real farms. Seed priming effectiveness varies considerably according to the plant species or genotype, type of priming agents and environmental conditions during seed treatment. For example, depending on Central Research Institute for Dryland Agriculture, Hyderabad (CRIDA), difference of genotypes, the same primed treatment may not have similar effect and it brings about another problem in germination percentages and seedling vigour (Dutta, 2018; Mwale et al., 2003). One of the main challenges is the possible deleterious effect on seed storage after priming. Lengthy or inappropriately scheduled treatments can affect seed longevity; therefore, it is particularly important to fine-tune the priming protocols—something which is not always easily manageable in various field scenarios (Dutta, 2018). Chemical priming tools also create concern about pollution to environment or plant system being deployed as a chemical being unable to degrade further which leads to sustainable use. It is therefore, important to employ alternative environment friendly priming approaches like physical or biological priming (Bera et al., 2021). Even though significant progress has been made to improve the priming strategies, complete understanding of physiological and molecular mechanisms particularly for novel techniques such as nanoparticles or ionizing radiation is still in demand. This is lack of knowledge which can leave ambiguity during application and scaling up (Bera et al., 2021; Dutta, 2018). Despite contiguities, seed priming is cost-effective but logistically difficult for large scale application. Accurate priming procedures for extended fields, particularly in suboptimal conditions, can be difficult to achieve. Furthermore, other high-level priming methods might be less feasible in large number of cases, due to requirement of specialised equipment or conditions (J. Wang et al., 2022).

Like with seed priming itself could do better to be researchers here, investigating to make the priming easier and more consistent — and more sustainable. Overcoming these limitations is essential to achieve the full potential of seed priming as a treatment for improving crop productivity in a changing climate and sustainable agriculture demands (Bera et al., 2021; Dutta, 2018). Cutting-edge methodologies including molecular priming, nanotechnology, and omics techniques open up opportunities to improve priming in agriculture and beyond. Particularly, in the case of seed priming in agriculture, such technologies can enhance germination, early seedling growth and plant stress tolerance with potential benefits to sustainable agricultural practices.

Molecular priming is the pre-sowing treatments causing beneficial biochemical, physiological, and molecular changes in seeds. These may be beneficial for seed and plant performance under stress conditions. By using omics approaches such as genomics proteomics and metabolomics, scientists can discover the intricate molecular networks underlying seed priming. This fine understanding is useful to track molecular elements such as genes, proteins and metabolites that are associated with the seed development processes and stress responses. This know-how may be used for the development of targeted molecular priming methods, including genetic manipulation strategies such as CRISPR-Cas9 to improve desirable traits in crops varieties (Şimşek et al., 2024).

Seed priming in response to nanotechnology Nanotechnology for seed priming represents a new approach by providing targeted delivery systems of priming agents. Owing to the small size and high surface area, nanoparticles can also provide a homogeneous release of nutrients, hormones and protective agent thereby enhancing seed priming efficacy. Nanotechnology can further help in diagnosis and suppression of plant diseases as evident by its role in managing the citrus disease huanglongbing where nano-sensors and metal nanoparticles are used to enable precise diagnosis and control (Mubeen et al., 2024).

Furthermore, the potential of nanotechnology to design nano-structured materials which can be utilized in seed priming which help in minimizing the negative impact of environmental constraints on seeds (finishing with water) could be exploited. These materials are useful to provide priming agents in response to particular environmental cues, allowing the proper environment for seed germination and seedling growth. Such specific regulation on the delivery and timing of priming agents can contribute to better seed performance under diverse environmental conditions (Y Wang et al., 2024).

These are complementary advanced technologies capable of integrating the seed-priming strategies as much as possible. Molecular priming lays the bases and omics technologies/Nanotechnology improve and exacerbate the efficiency of priming effects. The convergence of these technologies may enable a paradigm shift in agriculture productivity and sustainability that can address food security in the context of climate changes and loss of biodiversity (M. A. Khan et al., 2024).

Looking to the future, seed priming will have a bright prospect in climate-resilient agriculture for increasing crop productivity and adopting sustainable practices in different agro-ecologies. Seed priming, being a pre-sowing treatment conditions seeds for germination by enhancing their abiotic stress tolerance to drought, salinity and extremes of temperature—typical under climate change parameters (Do Espirito Santo Pereira et al., 2021; Indurugalla et al., 2023).

Among the advancements applicable for seed-priming technique, the use of nanotechnology is one of much importance. Nanoparticles (NPs) promote seed nano-priming to activate the metabolism and signaling pathways of seeds, and enhance their germination, plant growth as well as stress tolerance. In addition, this method leads to diminishment of reliance on chemical fertilizers and pesticides that can be one way toward sustainable agricultural practices (Do Espirito Santo Pereira et al., 2021; Salam et al., 2022)

**Table 3. Emerging and sustainable seed priming technologies**

<b>Technology</b>	<b>Description</b>	<b>Advantages</b>	<b>Limitation</b>	<b>Reference</b>
<b>Nano-priming</b>	Nanoparticles deliver nutrients/hormones efficiently	Enhanced uptake, long-lasting effects	Safety/toxicity assessment needed	Nile et al. (2022); Do Espirito Santo Pereira et al. (2021)
<b>Molecular priming</b>	Pre-sowing activation of molecular networks	Induces stress memory, faster response	Expensive protocols	Şimşek et al. (2024)
<b>Bio-priming</b>	Seed inoculation with beneficial microbes	Improves soil microbiome and resilience	Strain-specific efficiency	Rajendra Prasad et al. (2016)

<b>Physical priming (Plasma, Magnetic)</b>	Non-chemical enhancement of seed metabolism	Eco-friendly, fast, no residues	Requires specialized equipment	Bera et al. (2021); Shelar et al. (2022)
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In addition, seed priming with botanical extract (e.g., seaweed extract and plant extract) provides a cost-effective and eco-friendly technology for other approaches. These extracts promote germination of seed and growth under stress condition, and offer a sustainable way for enhancing crop yield in the future (Indurugalla et al., 2023). Dryland restoration in arid and semi-arid areas that are most vulnerable to climatic change requires employing seed priming. It increases nutrient efficiency in plants, soil fertility, and facilitates stress tolerance and adaptation by the plants thereby rendering it unarguably important for eco-restoration (Jarrar et al., 2024). Despite their merits, several challenges persist: (i) whether and to which extent such techniques can be scaled up, (ii) environmental impacts, and (iii) fine-tuning of priming protocols for different agroecosystems (Chatterjee et al., 2018; M. A. Khan et al., 2024). Studies are in progress to develop affordable, sustainable priming methods and the genetic and molecular mechanisms underlying stress tolerance that might result in even more effective climate-resilient agriculture in the future (Nile et al., 2022; Shelar et al., 2022). Seed priming shows immense potential for increasing climate resilience in agriculture and novel methods such as nano-priming, and cold plasma treatments are pioneering the way toward a sustainable food supply (Shelar et al., 2022).

## **9. Conclusion**

Seed priming is an important approach to improve germination and protect crop yield under abiotic stress conditions. The major conclusion is that seed priming can efficiently increase the germination percentage, seedling growth and stress resistance. This is achieved through cellular level physiological and biochemical changes. These changes involved, among others, higher enzymatic activities, richer antioxidant reserves and better hormonal regulation (Jatana et al., 2026; Louis et al., 2022). Priming activates pregerminative metabolism, enhances seedling defense and increases plant robustness. Techniques like hydropriming, osmopriming, hormonal priming and

nanoparticle priming have been known to provide defense against multiple environmental stress factors such as high temperature, drought and salinity (Jatana et al., 2024; Nie et al., 2022). Seed priming has also been shown to be effective in developing transgenerational stress memory through epigenetic and chromatin modification that make the plants of next generation better adapted under stressful conditions (Louis et al., 2023). Seed priming must be emphasized for sustainable crop production because of its effectiveness, economy, and environmental compatibility. It offers a feasible solution for farmers to increase crop yield and the resilience of crops in relation to climate change. The seed priming may be a key player in searching the principles of agricultural sustainability by saving input needs and enhancing crop resistance against changing climate, which eventually leads to more stable-yielding and higher rice production (M. O. Khan et al., 2022; Sen & Das, 2024).

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