

Sustainable Wheat Production: Seed Priming for Abiotic Stress Resilience

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Abstract

Wheat production is crucial for global food security, but it is frequently hampered by abiotic stress and adverse conditions, particularly as a result of climate change. To enhance crop resilience, farmers and seed companies are focused on seed priming technology to improve agronomic performance in adverse conditions. Seeds undergo significant physiological, biochemical, and molecular changes that allow them to germinate and thrive under stress conditions. Recent approaches to hydropriming, osmopriming, chemopriming, hormopriming, nanopriming, biopriming, and physical priming procedures have shown promising biological improvements, reducing impacts of saltiness, metals, stress from floods, and enhancing resilience to heat, drought, cold, and phytopathogens. This emphasizes the importance of seed priming technology in increasing crop plant production under adverse environmental conditions and meeting global food demand.

Keywords: High quality seeds; Seed priming; Stress tolerance; Wheat; Biotic/Abiotic stress; Seed priming; Nanopriming.

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Introduction

Wheat is an extensively cultured crop that possesses a substantial quantity of nutrients for human consumption (Erenstein et al., 2022). Climate change-related ecological stress may lead to a 28.9% reduction in wheat yield, although demand is projected to upsurge by 61% by 2050 to accommodate a demographic expansion (Long et al., 2022). Microbial and environmental stress have significant effects on wheat, reducing the yield of grains and quality of protein by 58.5% and 48.6%, respectively. Fluctuations in rain and high temperatures during the growing season have lowered the yield of wheat (Tirfi & Oyekale, 2022). Throughout their lives, crop plants are subjected to a range of biotic and abiotic stressors at the field level, such as air composition, temperature, dissolved solids, soil moisture, sunlight exposure, plant diseases, and pests. These elements are a major barrier to wheat production worldwide. Furthermore, their adverse impacts on wheat growth, development, and grain yield have been extensively researched (Zheng et al., 2020). As a result, these factors lower crop yields, disturb economic stability, and jeopardize the world's food security (Figure 1). To guarantee food security and better grain yields, techniques for improving the tolerance of plants and modification to future climates are urgently required (Wang et al., 2023).

In order to improve agronomic features and offset the harmful consequences of biotic and abiotic stressors on agricultural plant production, many researches have concentrated on static farming management measures, such as watering frequency, volume, fertilizer, pesticide level, and selecting resistant varieties. One practical, safe, and economical option for increasing agricultural yields is seed priming. Priming is a metabolic process that occurs in seeds before they germinate. It involves a number of changes at biochemical, physiological and molecular levels, and it activates genes that are related to germination and stress response. There is some evidence that "priming memory" may be linked to the development of stress tolerance through priming treatments. Depending on the circumstances that were antecedently applied to the seeds, priming memory can activate stress tolerance in them (Chen & Arora (2013). By following priming techniques, seeds are able to remember the last stress they experienced, which could help them develop tolerance to future pressures (Figure 2) (Liu et al., 2022). This chapter aims to synthesize the priming effects on wheat stress responses across generations, to shed light on the physiological mechanisms at work, and to offer suggestions for how future research might make this strategy more effective and long-lasting.

1. Mechanism of Priming

Seed germination is a complex process that encompasses various metabolic activities, leading to the transition from stored food reserves to the activation phase, during which the radicle and plumule develop (Kamithi et al., 2016). Seed priming strategies are starting to make a name for themselves as a practical and encouraging way to efficiently increase crop yields even when faced with challenging

environmental conditions (Rifna et al., 2019). Seed priming techniques enhance the morphophysiological profile, modulate phytohormones, reconfigure gene expression, and stimulate the metabolism of crucial enzymes (Marthandan et al., 2020). Germination transpires in three stages following the sowing of dry seeds: (I) imbibition, (II) pregermination, and (III) emergence (Zhao et al., 2018). The process of priming seed is recognized to induce 'pregermination' without the development of the radicle. Various antioxidants, containing peroxidase, ascorbate peroxidase, catalase and superoxide dismutase are typically activated throughout seed bioactivation processes. In addition to protecting cell membranes from ROS, these antioxidants reduce environmental stressors, promote healthy seed germination, and foster optimal seedling development (Hussain et al., 2016) (Fig. 3).

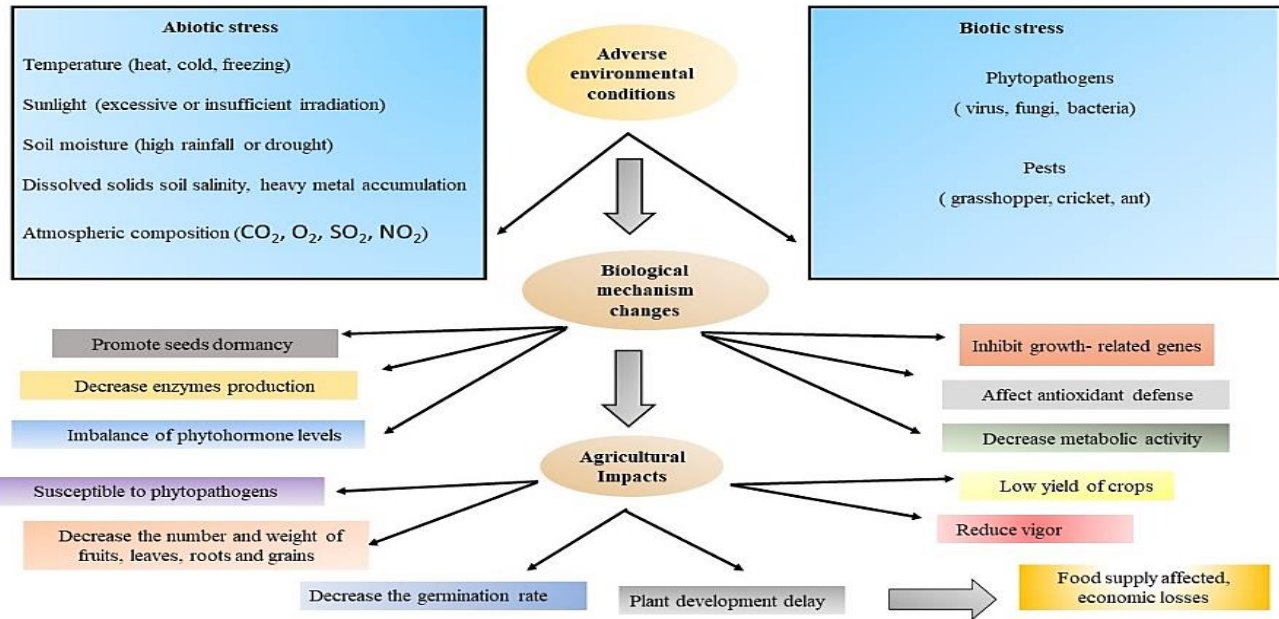


Fig. 1: Crop Yield, Food Security, And Economic Stability Are All Negatively Impacted When Unfavorable Environmental Factors Alter the Biological Mechanisms of Crops.

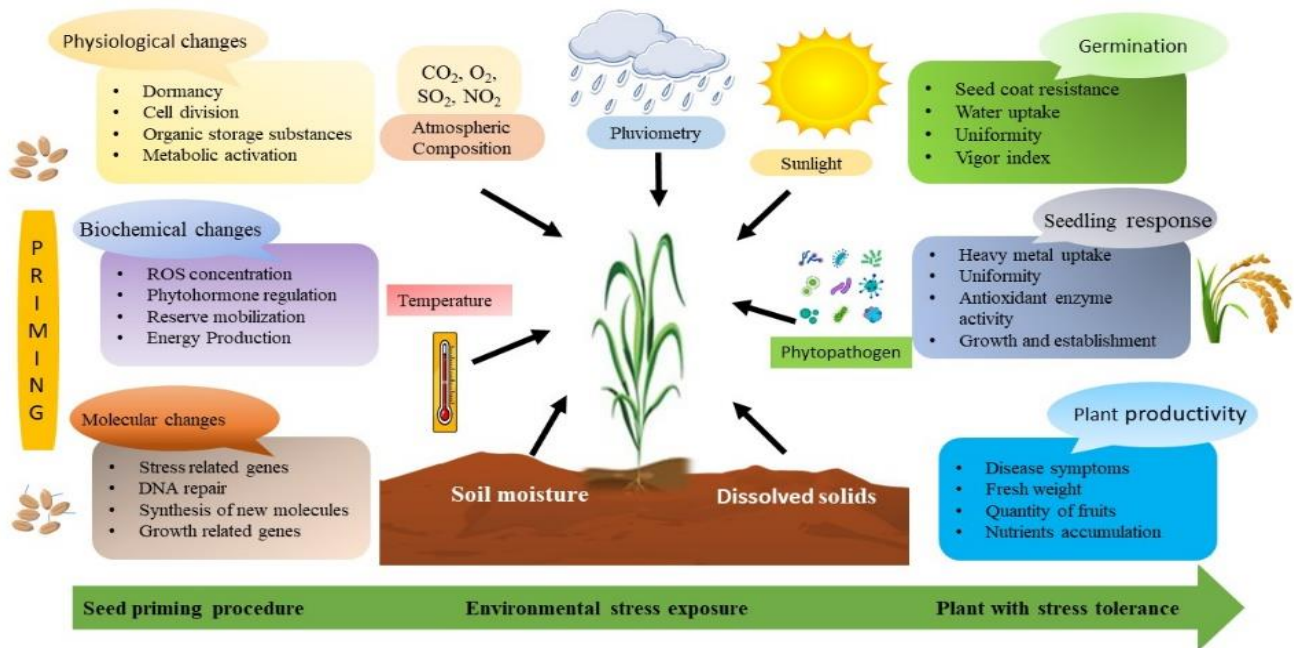


Fig. 2: Depicting The Process by Which Primed Seedlings Acquire Tolerance to Environmental Stress.

Farmers and seed firms have praised priming technology for its excellent agronomic performance with many different types of crop plants (Ibrahim, 2016). Priming seeds has several benefits for crop plants, and there have been few reports of any detrimental impacts on agriculture (Li et al., 2017). Agricultural solutions must be developed promptly to produce food effectively in light of rising food

demand, diminishing natural resources, and climate change (King et al., 2017). The purpose of this chapter is to conclude the most important methods of seed priming including physical priming, hydropriming, nanopriming, hormoprining, chemoprining, bioprining and osmoprining, with an eye toward improving agricultural plant production efficiency in challenging environments. This chapter represents recent progresses in seed priming technology and evaluates the agronomic potential of physiological, biochemical, and molecular methodologies.

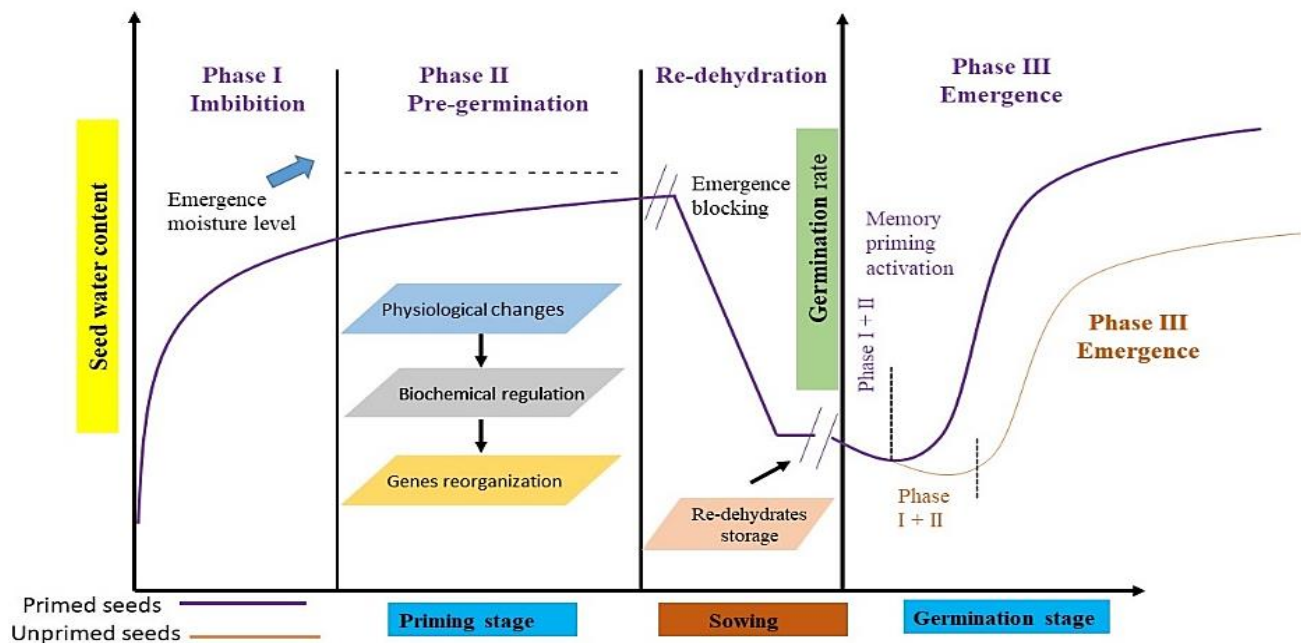


Fig. 3: The priming methods and its contrast to the germination outcomes of unprimed and primed seeds, depicted schematically. During the first phase, known as imbibition, messenger ribonucleic acid (mRNA) increases respiratory activity and protein synthesis through controlled water intake. Protein synthesis, metabolic processes, mitochondrial synthesis, soluble sugar alterations, repair mechanisms, and a host of other germination-related physiological, biochemical, and molecular processes take place during Phase II (pregermination), with the formation of radicles inhibited. For seed companies in particular, re-dehydration is an absolute necessity when postponing final sowing. When memory priming is activated in primed seeds, they perform better during phase III (emerging), whereas unprimed seeds spend more time in phases I and II.

2. Techniques of Priming

In order to produce crop plants in the face of challenging environmental conditions, this study offers a variety of evidence regarding seed priming strategies. A summary of various studies that looked at the impacts of stress on seed priming technology and how it affected crop plant production is provided in Table 1.

a. Hydropriming

Hydropriming enables proper germination and seedling growth; it is an economical, practical, environmentally and agronomically efficient method of overcoming numerous environmental stress conditions. Hydropriming is a straightforward process that requires imbibing the seeds in water at a specific temperature for a specific amount of time, either in darkness or light (Zhao et al., 2018). Plazek et al. (2018) his past research showed that hydropriming could help crops better withstand cold weather. This study used the hydropriming method, which involves three hours at 20°C, to examine the effects of a low temperature of 7°C on the biochemical and physiological changes that occur while seedling establishment. Reduction of cell membrane permeability, control of ABA concentration, and amylolysis activity all proved that hydropriming successfully protected seeds from cold damage during germination (Soleimanzadeh, 2013).

Hydropriming is extensively employed by seed producers to mitigate inconsistent seed germination and establishment due to adverse environmental circumstances, including dryness, saline soils, and heavy metal deposition (Wang Xiao et al., 2017). These stresses impair cell division and protraction, dwindle food absorption and translocation, and lower tissue hydration status and photosynthesis, ultimately leading to decreased enzymatic activity and excessive formation of reactive oxygen species (Forti et al., 2020). Plants initiate a self-defense process to safeguard cells from damage by regulating reactive oxygen species activities, including hydrogen peroxide. The seed hydropriming technique improved seed germination and seedling establishment in heavy metal polluted soil. The study successfully increased antioxidant activity (SOD and APX) and genes related to DNA repair (OGG1, 8-oxoguanine glycosylase, FPG, etc.) (Li et al., 2019).

In most cases, insufficient establishment and decreased crop production emerge as a consequence of anaerobic conditions that prevail throughout the germination and seedling growth processes. Mondal et al. (2020) examined the effect of hydropriming on the growth indices and physiological mechanisms of different crop genotypes when they were growing in anaerobic circumstances, from germination to seedling development. The germination and growth of rice seedlings in flooded soils were greatly enhanced by hydropriming. This study has shown

that hydropriming treatment speeds up the breakdown of stored carbs by raising the activity of enzymes that break down starch and keeping malondialdehyde (MDA) levels low (Mu et al., 2022).

b. Osmopriming

Osmopriming strategies, routinely employed by seed firms to augment seed vigor, have demonstrated favorable germination and plant growth outcomes under various adverse environmental circumstances, including cold, salt, and drought (Ferreira Ribas et al., 2019). In this method, seeds are submerged in a solution that has a low osmotic potential (ψ), which can be made of polyethylene glycol (PEG), sorbitol, mannitol, glycerol, or inorganic chemicals including $MgSO_4$, $CaCl_2$, K_2SiO_3 , KNO_3 , $NaCl$ and KCl . Less cellular damage occurs because the seeds soak slowly and absorb water. Tabassum et al. (2018) investigated osmopriming using a 1.5% $CaCl_2$ solution as part of their research on drought-tolerant wheat (*Triticum aestivum*) cultivation.

When compared to hydropriming treatments, the results showed that agricultural plant enhancement significantly improved osmolyte accumulation, tissue hydration, leaf area, and yield. Osmopriming enhanced promising plant responses by significantly reducing lipid peroxidation and increasing drought tolerance (Litalien & Zeeb, 2020).

Soil salinity is a detrimental factor that results in reduced agricultural yields, particularly in dry and semiarid areas. Soil salinity increases annually, primarily due to inadequate agronomic practices (Munns & Gilliham, 2015). Salinity stress induces elevated osmotic pressure, unbalanced ion absorption, and antioxidant imbalance in sorghum, hence impairing onset of growth and reducing crop yield (Kopittke et al., 2019). Recent findings indicate that wheat seeds osmoprimed with potassium silicate (K_2SiO_3) are the most proficient means to mitigate the adverse effects of salt stress during germination and plant development (Feghhenabi et al., 2020).

Reportedly, low temperatures in wheat lead to higher concentrations of reactive oxygen species (ROS) in the seeds, which disrupts various biological processes and creates an asymmetry between the light-absorbing capacity of the leaves and the energy-releasing capacity of the cells, making it difficult for the plants to carry out vital metabolic processes. Taking into account the fact that, owing to both population growth and environmental changes, wheat is expected to have a high demand in the years to come. Li et al. (2019) enhanced the cryoresistance of wheat plants by the use of osmopriming therapy in seeds (30mM $NaCl$). Priming effectively reduced MDA buildup and alleviated cell death, enhancing photochemical efficiency in seedlings. Primed seeds have higher germination ability when MDA activity is lower because lipid peroxidation is reduced. This, in turn, helps to retain the integrity of the membrane (Bhardwaj et al., 2016).

c. Chemopriming

Chemopriming is a technique employed to enhance seed quality and augment resilience to environmental stressors. The process utilizes inorganic compounds such as hydrochloric acid, selenium, fungicides, and insecticides, as well as organic materials including crude plant extracts, essential oils and dairy products (Moulick et al., 2016). Chemopriming induces biochemical alterations, including enhanced antioxidant activity, which diminishes heavy metal absorption and augments tolerance to freezing, salt, and drought stress in agricultural crops (Valivand et al., 2019). Extremely cold circumstances markedly diminish the germination index, impairing seedling growth by inhibiting starch metabolism and respiration rate. Research indicates that selenium treatment is among the most efficacious interventions, enabling rice to flourish under cold stress. Chemopriming also increases the levels of glutathione and free proline, so strengthening the antioxidative defense mechanism. In agricultural practices, elevated concentrations of arsenic-contaminated groundwater can inhibit normal growth, resulting in a 70% reduction in germination rates. Chemopriming can improve germination, shoot length, and seedling biomass in arsenic stress settings (Hozayn et al., 2020).

d. Hormopriming

Phytohormones inherently regulate biological mechanisms in plant species (Shu et al., 2016). Strigolactones, jasmonates, brassinosteroids, abscisic acid, auxin, cytokinins, ethylene, gibberellins, jasmonates, salicylic acid, and strigolactones are phytohormones that regulate seed quiescence, germination, plant development, and defense mechanisms against environmental stresses. These compounds have undergone experimental evaluation to assess plant responses to adverse environmental conditions, potentially aiding in the creation of tools and protocols for improving agricultural output (Madany et al., 2020). Hormopriming is a technique that is commonly used by seed producers to improve the stress tolerance of crop species. This technique is used to encourage drought tolerance in maize, cold shock tolerance in rice and salt tolerance in wheat. GAs and ABA both are responsible for regulating a variety of physiological, biochemical, and molecular processes in tomato plants. These processes include germination, seedling development, nutrient transport and allocation, and the reprogramming of gene expression. By gaining an understanding of the fluctuations that occur in phytohormones and gene expression during the process of seed invigoration and seed emergence, it is possible to facilitate the development of new ideas and technologies that can improve agronomic characteristics (Moori et al., 2020).

Cold and dry conditions can induce cellular damage and diminish carbohydrates, lipids, and proteins, resulting in significant economic losses. Previous studies examined the impact of seed hormopriming on chilling stress in relation to crop germination and seedling growth, demonstrating improved germination performance and enhanced morphological characteristics. The exogenous administration of salicylic acid and methyl jasmonate in seeds demonstrated an enhancement of biochemical and physiological traits under drought stress relative to hydropriming. Under drought conditions, Samota administered methyl jasmonate or salicylic acid to desiccation-resistant and desiccation-sensitive plants, and the plants' growth and development were improved as a result of the alleviation of the negative effects of aridification (Samota et al., 2017).

e. Nanopriming

Nanotechnology is a refined approach in agriculture, demonstrating favorable agronomic outcomes for several crop species. Over the past

few decades, nanoparticles have exhibited increased biological efficacy in plants through nanofertilizers and diminished harmful effects of nanoherbicides and nanopesticides (Sharma et al., 2020). Nanoprimering agents, including zinc oxide and silver nanoparticles, have been employed in many plant species to improve seedling recruitment and germination indices: *Carthamus tinctorius*, *O. sativa*, *Thymus kotschyanus* and *Citrullus lanatus* (Singh et al., 2020). Furthermore, nanoprimering is among the most effective techniques for augmenting salinity tolerance in plants by improving biochemical and physiological responses. Shafiq et al. (2021) observed enhancements in the agronomic characteristics of wheat plants subjected to fullereneol nanoprimering (0, 15, 45, 85, and 120nM concentrations) under saline stress (150 mM NaCl). The chapter demonstrated that fullereneol enhanced the uptake of K^+ , Ca^{2+} , and P, resulting in enriched ionic and ROS equilibrium and facilitating grain yield recovery through plant stress resilience.

f. Bioprimering

Bioprimering, though not extensively utilized in crop production, is an innovative, environmentally sustainable technique involving the application of strains such as *Bacillus* spp., *Enterobacter* spp., *Pseudomonas* spp., and *Trichoderma* spp. to seeds, enhancing germination rates, uniformity, seedling vigor, and growth metrics (Paparella et al., 2015). This strategy involves inoculating seeds with beneficial microbes that colonize the rhizosphere, thereby diminishing seed and soil-borne diseases and enhancing endophytic connections with the plant (Rozier et al., 2019). Although there is limited research on bioprimering which has demonstrated significant beneficial potential between plants and microbes in enhancing biotic and abiotic tolerance in crop production (Rozier et al., 2019).

In order to strengthen the plant's defence mechanisms, mycorrhizal fungus can naturally cause a number of important proteins and RNAs to clump together in the roots (Shukla et al., 2015). In a separate bioprimering experiment, *Trichoderma harzianum* improved resistance to plant pathogens and drought resilience in wheat through physiological defense mechanisms. Furthermore, Meena et al. (2016) showed improvements in height, root length, yield, and chlorophyll content in wheat when utilizing *Trichoderma* as a bioprimering agent across various soil conditions. The study identified an enhancement in nitrogen use efficiency, a significant agronomic characteristic, because leakage, runoff from surfaces, vaporization, denitrification, and bacterial absorption all result in the loss of over 50% of fertilizer utilized in intensive farming practices (Meena et al., 2015). Bioprimering has been considered as a disease control strategy, as endophytic bacteria can mitigate biotic stress hence, enhancing the biological system's defense against phytopathogens (Sun et al., 2019).

g. Physical Primering

i. Heat/Cold Primering

Thermal stress can profoundly affect agricultural output and worldwide food security. Inappropriate ambient temperatures during seed germination, seedling development, and vegetative phases can adversely affect yield productivity through physiological, biochemical, and molecular alterations. Effective photosynthesis and photosynthetic partitioning are crucial for plant growth; yet, heat stress can impair chloroplast architecture, reducing chlorophyll levels and resulting in diminished crop yields (Baier et al., 2019). Heat and cold primering strategies expose seeds to varying temperatures for a specified duration, hence activating biological systems including osmolytes and antioxidative defenses. Heat primering activates stress-responsive proteins and reconfigures metabolic homeostasis, providing substantial thermotolerance that enables plants to endure additional heat shocks. Nevertheless, the majority of heat/cold primering studies are performed on somatic tissues and infrequently on seeds (Adhikari et al., 2020a). Prior research indicates that moderate temperature as a primering intervention can enhance stress resilience under elevated temperatures in several crops and mitigate cold stress. Cryoresistance was shown in invigorated plants throughout the seed formation stage, suggesting that this technique may facilitate the induction of thermotolerance in crop species in places experiencing elevated temperatures (Thakur et al., 2020).

ii. Cold Plasma Primering

Cold plasma is a primering approach that is both inexpensive as well as beneficial for the environment, and it is also successful in increasing crop plant output (Adhikari et al., 2020b). A mixture consisting of neutral gas, ionized gas, electrons and positively charged particles is applied to seeds during the process of cold plasma primering. This mixture causes changes in the biological mechanisms that are involved, such as the density of reactive nitrogen species, electrical conductivity, the catabolism of phytohormones and reactive oxygen species (Ling et al., 2015). Primering, according to many authors, does more than just remove phytopathogen contamination; it also changes the seed's surface and makes it more water-absorbing, which breaks dormancy and triggers changes in hormones, proteome, secondary metabolites, and tissue differentiation. All of this leads to faster germination, better seedling growth, and greater resistance to environmental stress (Ghasempour et al., 2020).

Previous research demonstrated that cold plasma exposure augmented physiological and biochemical responses in many crop plants, including *T. aestivum*, *A. sativa*, *O. sativa*, *Gossypium hirsutum*, *Pisum sativum*, and *Cucurbita pepo* (Khatami & Ahmadiania, 2018). Seeds treated with cold plasma exhibit enduring benefits during subsequent stages, including the seedling phase, enabling them to withstand biotic and abiotic stresses, such as water scarcity and ailment. Despite the encouraging outcomes of cold plasma seed primering in crop productivity, the biological alterations and their regulatory mechanisms in various crop species alleviate living and non-living stress which are not well understood. Future research could concentrate on plasma-induced alterations in the cellular transcriptional programs of genes, hormone concentrations, and proteomic aspects, enhancing understanding of the intricate biological mechanisms affecting crop plants under stress, given the recent advancements in plasma technologies (Zhou et al., 2020).

3. Research Gaps and Future Perspectives

It is imperative to create new technologies that are viable, economical, environment friendly, and agronomically efficient in order to boost crop plant production in light of climate change, finite natural resources, and the world's growing population. Research indicates that primering

seeds to improve stress tolerance leads to increased crop yield. Future research on seed priming approaches might focus on a molecular basis, using a proteomic and/or metabolomics approach, for detecting and tracking stress-responsive genes before and after priming, and additionally during plant development. To improve agricultural yields in areas with unfavorable environmental circumstances, these kinds of studies might provide useful information about the priming technique for different plant species. Furthermore, this study strongly recommends researchers to combine two or more priming processes since this priming technique may be useful for effectively activating biological processes and increasing tolerance to numerous biotic/abiotic stresses. Ultimately, seed corporations may broadly implement priming techniques as a fundamental approach for increasing crop yield under severe environmental conditions.

Table 1: Different Seed Priming Strategies for Increasing Crop Productivity in Stressful Environments.

Crop species	Stress condition	Priming procedure	Crop performance & biological mechanisms change	Germination and seedling growth response	Reference
Hydropriming					
Wheat	Five days of heat stress at 42/24°C day/night; six days of drought stress with 16% plant accessible water; combination of heat and drought stress.	24% of plant- available water during the fifth leaf stage for a duration of 12 days	ABA; JA; MYC2; inhibited H3K4me3; MED25	RNA polymerase II; exhibited elevated chlorophyll concentration, resulting in an enhanced photosynthetic rate, grain production, and agronomic nitrogen-use efficiency during post-anthesis drought and thermal stress.	Liu & Avramova, 2016
Osmoprimering					
Chamran/Wheat	Saltwater from Lake Urmia (Iran) diluted to generate salinities electrical conductivities of 2, 4, 6, 8, 10, 12, 14, and 20 dSm ⁻¹ , while distilled water (EC≈0 dSm ⁻¹) was used for the control	Saltwater from Lake Urmia saline water was diluted to 200 mg L ⁻¹ of salt concentration for 10h), Potassium silicate (0, 1, 1.5, 2 mM for 6 h)	Enhanced salt resistance; augmented vitality index of plant growth, alongside improved length and weight.	Augmented seed viability along with enhanced seedling development.	Feghhenabi et al. (2020)
<i>Triticum aestivum</i> /Wheat	Low-temperature stress (2°C for 24h)	NaCl solutions (10, 30, and 50mM)	Enhanced crop performance: leaf area, tissue hydration status, osmolyte buildup, grain yield, and augmented drought resistance.	No germination responses were recorded	Li et al. (2019)
<i>Triticum aestivum</i> /Wheat	Drought stress (50% field capacity)	CaCl ₂ solution (1.5% for 12h)	Improvement of photochemical performance improves cold resistance; priming reduces MDA buildup and mitigates cell death.	No germination responses were recorded	Tabassum et al. (2018)
Chemoprimering					
<i>Triticum aestivum</i> cv. Kohistan-97 and cv. Pasban-90/Wheat	Drought stress	Sodium selenate solutions (25, 50, 75, and 100µM for 1/2 or 1h at 25°C)	Root length, dry matter, and plant biomass increased; total amount of free amino acids and total amount of sugar were elevated.	No germination responses were recorded	Nawaz et al. (2013)
Hormoprimering					
<i>Triticum aestivum</i> (cv. Millat 2011)/Wheat	Salinity stress solution)	Salicylic acid (125, 250, 375, and 500ppm)	Improved starch metabolism augmented the antioxidant enzyme activity, decreased the lipid peroxidation, hence promoting tolerance to stress and strong growth in plants.	No germination responses were recorded	Hussain et al. (2018)
Nanoprimering					

<i>Triticum aestivum</i> /Wheat	Cadmium stress	Zinc oxide nanoparticles (0, 25, 50, 75, and 100 mg L ⁻¹) or iron nanoparticles (0, 5, 10, 15, and 20 mg L ⁻¹)	Plant characteristics and productivity were augmented; photosynthetic response was boosted; electrolyte leakage was reduced; and activities of superoxide dismutase and peroxidase were improved.	No germination responses were recorded	Rizwan et al. (2019)
Biopriming					
<i>Triticum aestivum</i> /Wheat	Drought stress	Trichoderma harzianum strain	Augmented root vigor and shoot development; improved drought resistance through the reduction of MDA and hydrogen peroxide, alongside an elevation in total phenolic content.	No germination responses were recorded	Timmusk et al. (2014)
<i>Triticum aestivum</i> /Wheat	Drought stress	Rhizosphere Bacteria	Enhanced plant characteristics, biomass yield, and photosynthetic activity	Improved the germination rate	Shukla et al. (2015)
Physical priming					
<i>Triticum aestivum</i> cv. Yangmai 16/Winter wheat	Heat stress (day/night temperature of 35/27 °C)	Heat-shock (40°C for 4h)	Mitigated reductions in kernel weight and grain yield through improved photosynthetic capabilities, alongside the expression of stress-related genes.	Physiological and biochemical activities enhanced during germination	Zhang et al. (2016)
<i>Triticum aestivum</i> /Wheat	Cadmium contamination	Cold plasma (Ar/O ₂ and Ar/Air)	Seeds exhibited notable advancements in terms of morphology and total chlorophyll production, a substantial decrease in root and shoot cadmium concentration was detected, as well as decreased and blistered the seed coat, levels of cadmium transporters in the root (TaLCT ₁ and TaHMA ₂) and an increase in antioxidant enzymes.	No germination reactions were observed. Although cadmium plasma treatment degraded and blisters the seed coat, and lowered the pH of the seeds substantially.	Kabir et al. (2019)

References

- Adhikari, B., Adhikari, M., & Park, G. (2020a). The effects of plasma on plant growth, development, and sustainability. *Applied Sciences*, 10(17), 45-60.
- Adhikari, B., Adhikari, M., Ghimire, B., Adhikari, B. C., Park, G., & Choi, E. H. (2020b). Cold plasma seed priming modulates growth, redox homeostasis and stress response by inducing reactive species in tomato (*Solanum lycopersicum*). *Free Radical Biology and Medicine*, 156, 57-69.
- Baier, M., Bittner, A., Prescher, A., & van Buer, J. (2019). Preparing plants for improved cold tolerance by priming. *Plant, Cell & Environment*, 42(3), 782-800.
- Bhardwaj, J., Anand, A., Pandita, V. K., & Nagarajan, S. (2016). Pulsed magnetic field improves seed quality of aged green pea seeds by homeostasis of free radical content. *Journal of Food Science and Technology*, 53, 3969-3977.
- Chen, K., & Arora, R. (2013). Priming memory invokes seed stress-tolerance. *Environmental and Experimental Botany*, 94, 33-45.
- Erenstein, O., Jaleta, M., Mottaleb, K.A., Sonder, K., Donovan, J., Braun, H.J., 2022. Global trends in wheat production, consumption and trade. Wheat improvement: Food security in a changing climate. Springer International Publishing, Cham, pp. 47-66.
- Feghhenabi, F., Hadi, H., Khodaverdiloo, H., & Van Genuchten, M. T. (2020). Seed priming alleviated salinity stress during germination and emergence of wheat (*Triticum aestivum*). *Agricultural Water Management*, 231, 106022.
- Ferreira Ribas, A., Volpi e Silva, N., Dos Santos, T. B., Lima Abrantes, F., Castilho Custodio, C., Barbosa Machado-Neto, N., & Esteves Vieira, L. G. (2019). Regulation of α -expansins genes in Arabidopsis thaliana seeds during post-osmopriming germination. *Physiology and Molecular Biology of Plants*, 25, 511-522.
- Forti, C., Shankar, A., Singh, A., Balestrazzi, A., Prasad, V., & Macovei, A. (2020). Hydropriming and biopriming improve *Medicago truncatula* seed germination and upregulate DNA repair and antioxidant genes. *Genes*, 11(3), 242.
- Ghasempour, M., Iranbakhsh, A., Ebadi, M., & Oraghi Ardebili, Z. (2020). Seed priming with cold plasma improved seedling performance, secondary metabolism, and expression of deacetylindoline O-acetyltransferase gene in *Catharanthus roseus*. *Contributions to Plasma Physics*, 60(4), e201900159.
- Hozayn, M., Abd-Elmonem, A. A., & Samaha, G. M. (2020). The physiological effect of pre-soaking with tryptophan on sugar beet (*Beta vulgaris*) productivity under different levels of salinity stresses. *Bulletin of the National Research Centre*, 44, 1-9.
- Hussain, S., Khaliq, A., Tanveer, M., Matloob, A., & Hussain, H. A. (2018). Aspirin priming circumvents the salinity-induced effects on wheat emergence and seedling growth by regulating starch metabolism and antioxidant enzyme activities. *Acta Physiologiae Plantarum*, 40, 1-12.
- Hussain, S., Yin, H., Peng, S., Khan, F. A., Khan, F., Sameeullah, M., & Nie, L. (2016). Comparative transcriptional profiling of primed and non-

- primed rice seedlings under submergence stress. *Frontiers in Plant Science*, 7, 1125.
- Ibrahim, E. A. (2016). Seed priming to alleviate salinity stress in germinating seeds. *Journal of Plant Physiology*, 192, 38-46.
- Kabir, A. H., Rahman, M. M., Das, U., Sarkar, U., Roy, N. C., Reza, M. A., & Uddin, M. A. (2019). Reduction of cadmium toxicity in wheat through plasma technology. *PLoS One*, 14(4), e0214509.
- Kamithi, K. D., Wachira, F., & Kibe, A. M. (2016). Effects of different priming methods and priming durations on enzyme activities in germinating chickpea (*Cicer arietinum*). *American Journal of Natural and Applied Sciences*, 1(1), 1-9.
- Khatami, S., & Ahmadiania, A. (2018). Increased germination and growth rates of pea and Zucchini seed by FSG plasma. *Journal of Theoretical and Applied Physics*, 12(1), 1-15.
- King, T., Cole, M., Farber, J. M., Eisenbrand, G., Zabarar, D., Fox, E. M., & Hill, J. P. (2017). Food safety for food security: Relationship between global megatrends and developments in food safety. *Trends in Food Science & Technology*, 68, 160-175.
- Kopittke, P. M., Menzies, N. W., Wang, P., McKenna, B. A., & Lombi, E. (2019). Soil and the intensification of agriculture for global food security. *Environment International*, 132, 105078.
- Li, H., Li, H., Lv, Y., Wang, Y., Wang, Z., Xin, C., & Li, X. (2019). Salt priming protects photosynthetic electron transport against low-temperature-induced damage in wheat. *Sensors*, 20(1), 62-76.
- Li, Z., Xu, J., Gao, Y., Wang, C., Guo, G., Luo, Y., & Hu, J. (2017). The synergistic priming effect of exogenous salicylic acid and H₂O₂ on chilling tolerance enhancement during maize (*Zea mays*) seed germination. *Frontiers in Plant Science*, 8, 11-33.
- Ling, L., Jiangang, L., Minchong, S., Chunlei, Z., & Yuanhua, D. (2015). Cold plasma treatment enhances oilseed rape seed germination under drought stress. *Scientific Reports*, 5(1), 1-10.
- Litalien, A., & Zeeb, B. (2020). Curing the earth: A review of anthropogenic soil salinization and plant-based strategies for sustainable mitigation. *Science of the Total Environment*, 698, 134235.
- Liu, H., Able, A. J., & Able, J. A. (2022). Priming crops for the future: Rewiring stress memory. *Trends in Plant Science*, 27(7), 699-716.
- Liu, N., & Avramova, Z. (2016). Molecular mechanism of the priming by jasmonic acid of specific dehydration stress response genes in Arabidopsis. *Epigenetics & Chromatin*, 9, 1-23.
- Long, X. X., Ju, H., Wang, J. D., Gong, S. H., & Li, G. Y. (2022). Impact of climate change on wheat yield and quality in the Yellow River Basin under RCP8.5 during 2020–2050. *Advances in Climate Change Research*, 13(3), 397-407.
- Madany, M. M., Zinta, G., Abuelsoud, W., Hozzein, W. N., Selim, S., Asard, H., & Abd Elgawad, H. (2020). Hormonal seed-priming improves tomato resistance against broomrape infection. *Journal of Plant Physiology*, 250, 153184.
- Marthandan, V., Geetha, R., Kumutha, K., Renganathan, V. G., Karthikeyan, A., & Ramalingam, J. (2020). Seed priming: a feasible strategy to enhance drought tolerance in crop plants. *International Journal of Molecular Sciences*, 21(21), 8258.
- Meena, R. K., Singh, R. K., Singh, N. P., Meena, S. K., & Meena, V. S. (2015). Isolation of low temperature surviving plant growth-promoting rhizobacteria (PGPR) from pea (*Pisum sativum*) and documentation of their plant growth promoting traits. *Biocatalysis and Agricultural Biotechnology*, 4(4), 806-811.
- Meena, S. K., Rakshit, A., & Meena, V. S. (2016). Effect of seed bio-priming and N doses under varied soil type on nitrogen use efficiency (NUE) of wheat (*Triticum aestivum*) under greenhouse conditions. *Biocatalysis and Agricultural Biotechnology*, 6, 68-75.
- Mondal, S., Khan, M. I. R., Entila, F., Dixit, S., Sta. Cruz, P. C., Panna Ali, M., ... & Ismail, A. M. (2020). Responses of AG1 and AG2 QTL introgression lines and seed pre-treatment on growth and physiological processes during anaerobic germination of rice under flooding. *Scientific Reports*, 10(1), 10214.
- Moori, S., & Ahmadi-Lahijani, M. J. (2020). Hormopriming instigates defense mechanisms in Thyme (*Thymus vulgaris*) seeds under cadmium stress. *Journal of Applied Research on Medicinal and Aromatic Plants*, 19, 100268.
- Moullick, D., Ghosh, D., & Santra, S. C. (2016). Evaluation of effectiveness of seed priming with selenium in rice during germination under arsenic stress. *Plant Physiology and Biochemistry*, 109, 571-578.
- Mu, Q., Cai, H., Sun, S., Wen, S., Xu, J., Dong, M., & Saddique, Q. (2021). The physiological response of winter wheat under short-term drought conditions and the sensitivity of different indices to soil water changes. *Agricultural Water Management*, 243, 106475.
- Munns, R., & Gilliham, M. (2015). Salinity tolerance of crops—what is the cost? *New Phytologist*, 208(3), 668-673.
- Nawaz, F., Ashraf, M. Y., Ahmad, R., & Waraich, E. A. (2013). Selenium (Se) seed priming induced growth and biochemical changes in wheat under water deficit conditions. *Biological Trace Element Research*, 151, 284-293.
- Paparella, S., Araujo, S. S., Rossi, G., Wijayasinghe, M. A. L. A. K. A., Carbonera, D., & Balestrazzi, A. (2015). Seed priming: State of the art and new perspectives. *Plant Cell Reports*, 34, 1281-1293.
- Plazek, A., Dubert, F., Kopec, P., Dziurka, M., Kalandyk, A., Pastuszek, J., & Wolko, B. (2018). Seed hydropriming and smoke water significantly improve low-temperature germination of *Lupinus angustifolius*. *International Journal of Molecular Sciences*, 19(4), 992.
- Rifna, E. J., Ramanan, K. R., & Mahendran, R. (2019). Emerging technology applications for improving seed germination. *Trends in Food Science & Technology*, 86, 95-108.
- Rizwan, M., Ali, S., Ali, B., Adrees, M., Arshad, M., Hussain, A., & Waris, A. A. (2019). Zinc and iron oxide nanoparticles improved the plant growth and reduced the oxidative stress and cadmium concentration in wheat. *Chemosphere*, 214, 269-277.
- Rozier, C., Gerin, F., Czarnes, S., & Legendre, L. (2019). Biopriming of maize germination by the plant growth-promoting rhizobacterium *Azospirillum lipoferum* CRT1. *Journal of Plant Physiology*, 237, 111-119.
- Samota, M. K., Sasi, M., Awana, M., Yadav, O. P., Amitha Mithra, S. V., Tyagi, A., & Singh, A. (2017). Elicitor-induced biochemical and molecular manifestations to improve drought tolerance in rice (*Oryza sativa*) through seed-priming. *Frontiers in Plant Science*, 8, 934.
- Shafiq, F., Iqbal, M., Ali, M., & Ashraf, M. A. (2021). Fullereneol regulates oxidative stress and tissue ionic homeostasis in spring wheat to improve net-primary productivity under salt-stress. *Ecotoxicology and Environmental Safety*, 211, 111901.

- Sharma, G., Kumar, A., Devi, K. A., Prajapati, D., Bhagat, D., Pal, A., & Saharan, V. (2020). Chitosan nanofertilizer to foster source activity in maize. *International Journal of Biological Macromolecules*, *145*, 226-234.
- Shu, K., Liu, X. D., Xie, Q., & He, Z. H. (2016). Two faces of one seed: Hormonal regulation of dormancy and germination. *Molecular Plant*, *9*(1), 34-45.
- Shukla, N., Awasthi, R. P., Rawat, L., & Kumar, J. (2015). Seed biopriming with drought tolerant isolates of *Trichoderma harzianum* promote growth and drought tolerance in *Triticum aestivum*. *Annals of Applied Biology*, *166*(2), 171-182.
- Singh, V. K., Singh, R., Tripathi, S., Devi, R. S., Srivastava, P., Singh, P., & Bhadouria, R. (2020). Seed priming: State of the art and new perspectives in the era of climate change. *Climate Change and Soil Interactions*, *8*, 143-170.
- Soleimanzadeh, H. (2013). Effect of seed priming on germination and yield of corn. *International Journal of Agriculture and Crop Sciences*, *5* (4)366-369.
- Sun, Q., Miao, C., Hanel, M., Borthwick, A. G., Duan, Q., Ji, D., & Li, H. (2019). Global heat stress on health, wildfires, and agricultural crops under different levels of climate warming. *Environment International*, *128*, 125-136.
- Tabassum, T., Farooq, M., Ahmad, R., Zohaib, A., Wahid, A., & Shahid, M. (2018). Terminal drought and seed priming improves drought tolerance in wheat. *Physiology and Molecular Biology of Plants*, *24*, 845-856.
- Thakur, A., Sharma, K. D., Siddique, K. H., & Nayyar, H. (2020). Cold priming the chickpea seeds imparts reproductive cold tolerance by reprogramming the turnover of carbohydrates, osmo-protectants and redox components in leaves. *Scientia Horticulturae*, *261*, 108929.
- Timmusk, S., Abd El-Daim, I. A., Copolovici, L., Tanilas, T., Kannaste, A., Behers, L., & Niinemets, U. (2014). Drought-tolerance of wheat improved by rhizosphere bacteria from harsh environments: enhanced biomass production and reduced emissions of stress volatiles. *PLoS One*, *9*(5), e96086.
- Tirfi, A. G., & Oyekale, A. S. (2022). Impact of climate change on yields of wheat in Ethiopia: An augmented Cobb-Douglas production function approach. *Journal of Agricultural, Food and Environmental Sciences*, *76*(1), 34-47.
- Valivand, M., Amooaghaie, R., & Ahadi, A. (2019). Seed priming with H₂S and Ca²⁺ trigger signal memory that induces cross-adaptation against nickel stress in zucchini seedlings. *Plant Physiology and Biochemistry*, *143*, 286-298.
- Wang Xiao, W.X., Liu Fulai, L.F., & Jiang Dong, J.D. (2017). Priming: a promising strategy for crop production in response to future climate. *Journal of Integrative Agriculture*, *16*(12), 2709-2716.
- Wang, X., Ge, J., He, M., Li, Q., Cai, J., Zhou, Q., & Jiang, D. (2023). Enhancing crop resilience: Understanding the role of drought priming in wheat stress response. *Field Crops Research*, *302*, 109083.
- Zhang, X., Zhou, Q., Wang, X., Cai, J., Dai, T., Cao, W., & Jiang, D. (2016). Physiological and transcriptional analyses of induced post-anthesis thermo-tolerance by heat-shock pretreatment on germinating seeds of winter wheat. *Environmental and Experimental Botany*, *131*, 181-189.
- Zhao, Y., Hu, M., Gao, Z., Chen, X., & Huang, D. (2018). Biological mechanisms of a novel hydro-electro hybrid priming recovers potential vigor of onion seeds. *Environmental and Experimental Botany*, *150*, 260-271.
- Zheng, Z., Hoogenboom, G., Cai, H., & Wang, Z. (2020). Winter wheat production on the Guanzhong Plain of Northwest China under projected future climate with SimCLIM. *Agricultural Water Management*, *239*, 106233.
- Zhou, R., Yu, X., Li, X., Dos Santos, T. M., Rosenqvist, E., & Ottosen, C. O. (2020). Combined high light and heat stress induced complex response in tomato with better leaf cooling after heat priming. *Plant Physiology and Biochemistry*, *151*, 1-9.