 doi:10.20944/preprints202109.0364.v1

Seed priming technology as a key strategy to increase crop plant production under adverse environmental conditions

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Abstract: Farmers and seed companies constantly require high-quality seeds with excellent agronomic performance. However, faced with environmental adversity, limited natural resources and increasing food demand around the globe, more attention has turned to improving crop plant production by implementing efficient strategies. Seed priming technology has shown promising biological improvements leading to suitable agronomic performance in crop plants under adverse environmental conditions. Seeds are subjected to controlled conditions that are conducive to complex physiological, biochemical, and molecular changes, conferring specific stress tolerance to subsequent germination and growth conditions. In this review paper, we aimed to study the recent approaches in the efficiency of hydropriming, osmopriming, chemopriming, hormopriming, nanopriming, matrix priming, biopriming, physical priming and hybrid priming procedures in the production of crop plants under environmental adversity, as well as their biological mechanism changes. All priming methods demonstrated relevant changes in the biological mechanism related to crop plant production by mitigating salinity effects, heavy metals, and flooding stress and enhancing chilling, heat, drought and phytopathogen tolerance. We strongly recommend that researchers combine multiple priming methods, known as hybrid priming, in their investigations to provide novel technologies and additional biological approaches to enhance the knowledge of crop plant science. Thus, the findings shed light on the use of seed priming technology as a key strategy to increase crop plant production under environmental adversity by acquiring stress tolerance and enhancing agronomic traits to meet the global food demand.

Keywords: stress tolerance; biological mechanisms; biotic/Abiotic stress; hybrid priming; high-quality seeds

1. Introduction

Faced with the increasing population and limited natural resources, climate change has imposed extra adverse conditions on crop plant production. This situation has worsened to the extent that food consumption has increased disproportionately to the population increasing in the last few years[1]. Moreover, it is predicted that by 2050, salinization consequences will affect 50% of arable lands in the world[2]. In terms of economic losses, environmental stressors have decreased crop production in developing countries, with USD 9.5 billion lost to diseases and pest infestation, USD 29 billion to drought, and USD 47 billion to other causes between 2005 and 2015, according to the FAO[3]. At the field level, during their lifespans, crop plants are exposed to several biotic and abiotic stressors such as temperature, sunlight, soil moisture, dissolved solids, atmospheric composition, phytopathogens and pests. Consequently, these factors reduce crop production, affect economic stability and threaten global food security (Fig. 1).

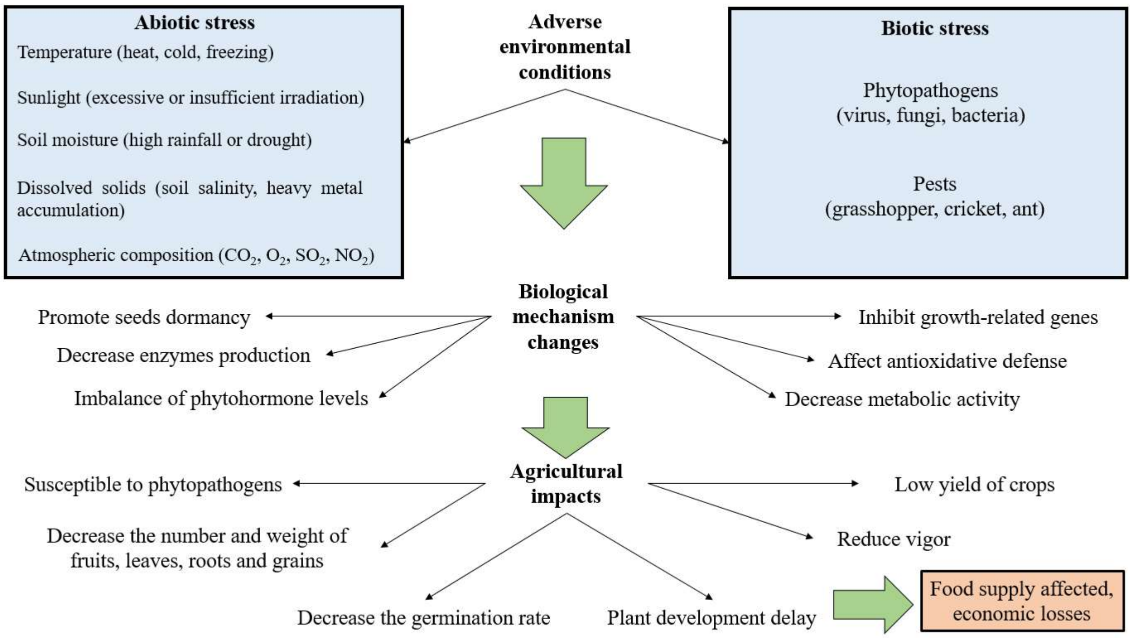

Figure 1. Adverse environmental conditions induce negative changes in biological mechanism of crops, affecting crop production, food supply and economic stability.

Among the several biological changes in crop plants that experience unsuitable environmental conditions, seed dormancy is considered one of the most common physiological consequences that significantly decrease crop production[4]. Dormancy is characterized by the inhibition of germination while waiting for favorable conditions[5]. In terms of phytohormones, germination and dormancy are controlled by the balance of hormone ratios, mainly ABA (abscisic acid) and GAs (gibberellins)[4,5]. These hormones are stimulated by specific growth-related genes, which in turn are down/upregulated mainly by environmental factors[6,7].

In an attempt to mitigate the negative impacts of biotic/abiotic stressors on crop plant production and increase agronomic traits, numerous studies have focused on static farming management, such as watering volume and frequency[8], fertilizer and pesticide amounts[9], and other techniques, including the use of resistant varieties[10]. Thus, among the several technologies available to increase crop production, one of the most feasible, low-risk and cost-effective is seed priming[11–16]. Seed priming is defined as a 'pregermination' metabolism inducing several physiological, biochemical, and molecular changes to activate stress-

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responsive genes associated with germination[17], in which the seed prepares for imminent environmental stress. Stress tolerance acquired through priming treatments has been suggested to possibly be associated with "priming memory". According to Chen and Arora[11], "priming memory" invokes stress tolerance in seeds depending on the conditions that were previously imposed on the seeds. In other words, seeds retain the preceding stress memory after the priming procedures, which may aid in the attainment of tolerance to subsequent stresses (Fig. 2).

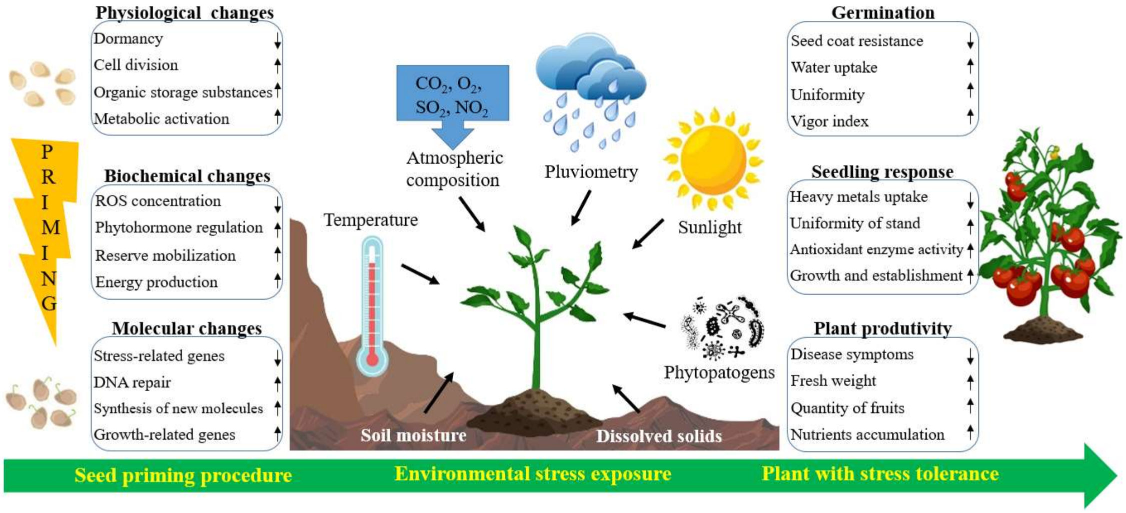

Figure 2. Schematic representation summarizing the mechanism underlying environmental stress tolerance acquired by primed seeds.

Seed priming technologies are emerging as a potential and promising method to increase crop production efficiently under unsuitable environmental conditions[13,16,18–21]. Seed priming methods are capable of improving the morphophysiological pattern, regulating phytohormones, reprogramming gene expression, and inducing the metabolism of important enzymes[13,22,23]. Germination occurs in three phases after the dry seeds are sown: (I) imbibition, (II) 'pregermination', and (III) emergence[14,24]. The procedure of seed priming is known to trigger 'pregermination' without radicle emergence. Different antioxidants, such as catalase (*CAT*), ascorbate peroxidase (*APX*), superoxide dismutase (*SOD*), and peroxidase (*POD*), are commonly triggered during seed priming procedures. These antioxidants protect cellular membranes against the harmful effects of reactive oxygen species (ROS) and help mitigate environmental stressors and improve seed germination and seedling growth[24,25] (Fig. 3).

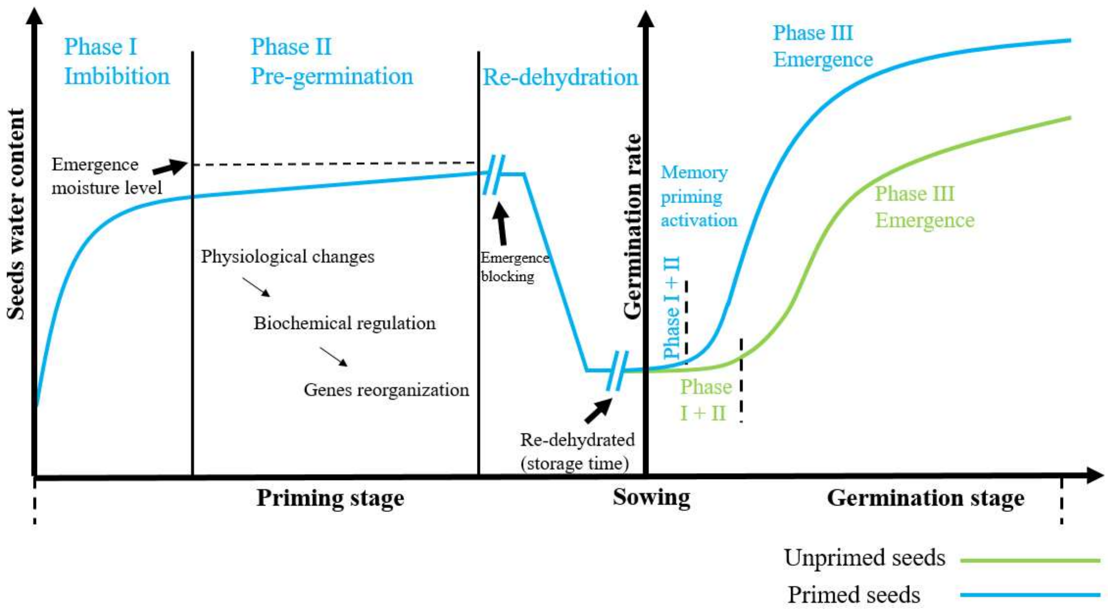

Figure 3. Schematic illustration of the seed priming process and comparison to the subsequent germination between unprimed seeds and primed seeds[13,14]. During phase I (imbibition), controlled water uptake allows the synthesis of protein and induces respiratory activities through messenger ribonucleic acid (mRNA). Phase II (pregermination) is related to several physiological, biochemical and molecular activities related to germination, such as protein synthesis, metabolic processes, mitochondrial synthesis, alterations in soluble sugars, and repair processes, but the emergence of radicles is prevented. Re-dehydration is necessary when the final sowing is postponed, in the case of seed companies. In primed seeds, phase III (emergence) is identified by memory priming activation, which results in better seed emergence performance, while unprimed seeds spend time performing phases I and II longer[14].

Priming technology has been appreciated by farmers and seed companies due to its great agronomic performance with a wide range of crop plants[13,16,24,26]. Several investigations have demonstrated the advantages of seed priming procedures in crop plant production[13,16,18–21], and reports of the negative effects of seed priming on agriculture remain scarce[27]. Considering the increasing food demand, limited natural resources and climatic change, the development of agricultural strategies is urgent to produce food efficiently[16,19,28–30]. In this context, the aim of this study is to summarize some of the main seed priming technologies: hydropriming, osmopriming, chemopriming, hormopriming, nanopriming, matrix priming, biopriming, physical priming and hybrid priming, referencing efficiency in the production of crop plants under adverse environmental conditions. The study also provides updated progress on seed priming technology as well as the agronomical potential of physiological, biochemical, and molecular approaches.

2. Seed priming technologies

The current study presents a wide range of evidence on the use of seed priming methods in crop plant production under adverse environmental conditions. In addition, a synopsis of several investigations on the biological effects of seed priming technology subjected to stress conditions and the impact on crop plant production is listed in Table 1.

2.1. Hydropriming

Hydropriming, an ecofriendly, feasible, agronomically efficient, and cost-effective procedure to overcome many environmental stress conditions, allows suitable germination and seedling growth in *Lupinus angustifolius* L.[31], *Oryza sativa*[32], and *Helianthus annuus* L.[33]. Hydropriming is a simple method that involves soaking the seeds in pure water for a particular period at a controlled temperature under dark or light conditions[14]. A previous investigation reported the potential of hydropriming to enhance tolerance to low-temperature conditions in *L. angustifolius*[31]. The study investigated the impact of low temperature (7 °C) on the physiological and biochemical changes during germination under the influence of the hydropriming method (3 h at 20 °C). The effectiveness of hydropriming in protecting seeds against cold damage during germination was confirmed due to reduced cell membrane permeability, amylolysis activity, and regulation of ABA content.

Hydropriming is widely used by seed companies to overcome irregular seed germination and stand establishment caused by unfavorable environmental conditions, such as drought, saline soils and heavy metal accumulation[19,34]. These stressors affect cell division and elongation, reduce nutrient uptake and translocation, and decrease tissue water status and photosynthesis, which consequently causes a reduction in enzymatic activity and overproduction of ROS[35]. To protect the cells from damage, plants activate a self-defense mechanism that controls ROS activities, such as H_2O_2[36]. Forti et al.[34] promoted better seed germination and seedling establishment of *Medicago truncatula* in soil contaminated with heavy metals via the seed hydropriming method. The study successfully upregulated genes involved in DNA repair, such as *OGG1* (8-oxoguanine glycosylase) and *FPG* (formamidopopyrimidine-DNA glycosylase) genes, and antioxidant activities (*SOD* and *APX*).

Anaerobic conditions during germination and seedling growth normally lead to poor establishment and low crop yield. Mondal et al.[32] investigated the responses of hydropriming to the growth index and physiological processes of rice genotypes during germination and seedling growth under anaerobic conditions. Hydropriming significantly enhanced the emergence and seedling growth of rice in flooded soils. According to the study, hydropriming treatment was able to improve the breakdown of stored carbohydrates by enhancing the enzymatic activities of starch catabolic enzymes and maintaining lower malondialdehyde (MDA) concentrations, as supported by other investigations[37].

2.2. Osmopriming

Routinely used by seed companies to enhance the vigor of seeds, osmopriming techniques have shown promising germination and plant growth performance[38,39] under several adverse environmental conditions, such as chilling[40], salinity[41,42] and drought[12]. In this method, seeds are immersed in an osmotic solution with low water potential (ψ) through the use of polyethylene glycol (PEG), mannitol, sorbitol, glycerol, or inorganic substances, such as NaCl, KCl, K_2SiO_3, KNO_3, $MgSO_4$, and $CaCl_2$. This immersion allows the seeds to absorb water slowly, thereby culminating in less cellular damage. Tabassum et al.[43] studied osmopriming (with 1.5% $CaCl_2$ solution) in the production of wheat (*Triticum aestivum* L.) under drought stress. The results revealed promising crop plant enhancement in comparison with hydropriming treatments regarding osmolyte accumulation, tissue water, leaf area, and yield. The positive plant responses were better with osmopriming due to a considerable decrease in lipid peroxidation and acquired drought tolerance. These results are in agreement with Chen and Arora[44], who discussed that the stress tolerance acquired by osmopriming is, in part, related to the gradual accumulation of proteins, such as dehydrins (DHNs), usually reported to protect against cellular dehydration, and a more robust antioxidant system in relation to the activation of pregerminative metabolism. DHNs (group 2 LEA proteins) are water-soluble lipid vesicle-associated proteins involved in the adaptive responses of plants to environmental stress tolerance[45]. Later, Chen et al.[46] successfully improved chilling and desiccation stress tolerance in *Spinacia oleracea* L. cv. Bloomsdale by osmopriming seeds. In this study, the authors associated stress tolerance with the accumulation of DHN-like proteins in spinach seeds, since they exclusively accumulated during the early phase of osmopriming in response to environmental stressors.

Soil salinity is another adverse condition that causes losses for crop plant production, especially in arid and semiarid regions[42]. Soil salinity becomes more extensive yearly, particularly as a result of inappropriate agronomic management[47,48]. Salinity stress conditions cause increasing osmotic pressure, ion uptake imbalanced, and oxidative stress in sorghum, hence affecting the early growth stages and decreasing crop production[49]. Recently, wheat seeds osmoprimed with potassium silicate (K_2SiO_3) was reported to be the most effective agent to relieve the negative impact of salinity stress during germination and plant growth[50]. Kubala et al.[41] detected improvements in the germination and seedling growth of *Brassica napus* primed with polyethylene glycol (-1.2 MPa) under salinity stress (NaCl: 100 mM). According to the study, the improvement of germination performance and seedling establishment in osmoprimed treatments was due to increased *P5CSA* gene expression and decreased *PDH* gene expression associated with proline accumulation and H_2O_2 concentrations. Further understanding of molecular markers is of interest for providing suitable protocols for seed priming programs for each plant species and local environmental constraints. Thus, this aspect is rather important because such molecular indicators linked with biological mechanism changes allow the prediction of seed quality and may provide further knowledge to support future studies and provide assistance to seed companies.

The consequences of low temperature in wheat are reported to be increased ROS concentrations in the seeds, which disturb several biological mechanisms and cause an imbalance between the ability of leaves to absorb light and release energy to the cells to perform essential metabolic activities[51,52]. Considering that there is an estimated high demand for wheat in the future due to the rising population[53] and climate change, Li et al.[40] improved the cold tolerance of wheat plants with osmopriming treatment in seeds (30 mM NaCl). The priming procedure successfully enhanced the photochemical efficiency in seedlings by decreasing MDA accumulation and alleviating cell death. Lower MDA activity indicates a decrease in lipid peroxidation, which maintains the integrity of the membrane and leads primed seeds to a better germination performance[54]. In another study, Zhang et al.[55] investigated the physiological and biochemical effects of osmopriming (PEG 8000 solution) on the germination performance and seedling establishment of sorghum [*Sorghum bicolor* (L.) Moench] under various soil moisture

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conditions. The experiment provided promising results concerning uniform emergence and decreased drought stress for suitable seedling establishment. The priming procedure strengthened the antioxidant activities of *POD*, *CAT*, *SOD*, and *APX*, which led to the enhancement of drought tolerance in sorghum plants.

2.3. Chemopriming

Chemopriming involves inorganic substances, such as hydrochloric acid (HCl), selenium (Se), fungicides and pesticides, or organic substances, such as essential oils, dairy products and crude plant extracts. Biochemical changes, such as antioxidant activity, are one of the most common improvements in seeds treated with chemopriming, leading to a reduction in heavy metal uptake[56], tolerance to chilling[57], salinity[58], and drought stress[59] in several crop plants[60].

Considered one of the most aggressive abiotic stresses, chilling conditions significantly decrease the germination index, leading to poor seedling growth of crop plants by reducing starch metabolism and lowering the respiration rate. Many crop plants are very sensitive to chilling stress during germination[61]. Hussain et al.[57] studied the physiological and biochemical mechanisms of rice cultivars primed with several methods and then subjected to chilling stress (18 °C). The application of selenium (50 μM) was shown to be one of the most effective treatments compared to osmopriming (calcium chloride: 100 mg L^{-1}), redox priming (hydrogen peroxide: 50 μM), and hormopriming (salicylic acid: 100 mg L^{-1}), allowing rice to thrive under chilling stress. The investigation also found that chemopriming treatment induced several physiological activities, such as peroxidase, catalase, and superoxide dismutase, and enhanced the accumulation of glutathione and free proline at the seedling stage, which provided a strong antioxidative defense system under chilling stress.

Another constraint experienced by farmers around the world, especially in Asian countries, is the high levels of arsenic-contaminated groundwater in rice cultivation, which is considered a limitation for normal rice growth, reducing germination by 70% in some cases. A study with chemopriming (selenium: 0.8 mg L^{-1}) treatment in rice under arsenic stress conditions demonstrated an enhancement of germination, shoot length, and seedling biomass [56]. In this case, the plant responses to chemopriming were reflected in the enhancement of biological mechanisms due to the reduction in arsenic uptake, hence suppressing oxidative damage by increasing antioxidant accumulation in rice seedlings. In another case with heavy metals in the soil, nickel stress resistance [at 50 ppm $Ni(NO_3)_2$] was detected in zucchini seedlings (*Cucurbita pepo* L. cv. Courgette d'Italie) by chemopriming with H_2S and $CaCl_2$ [62]. In this study, chemopriming induced postgerminative cross-adaptation by improving photosynthetic pigments and seedling biomass, as well as increasing the content of ascorbate, total thiols, and glutathione reductase activity in leaves, while ascorbate peroxidase activity decreased significantly.

2.4. Hormopriming

Phytohormones naturally mediate the regulation of biological mechanisms in plant species[4,63]. Abscisic acid, auxin, brassinosteroids, cytokinins, ethylene, gibberellins, jasmonates, salicylic acid, and strigolactones are phytohormones involved in regulating seed dormancy, germination and plant development, as well as defense responses to environmental stressors[4,64,65]. These substances have been evaluated in experimental studies to detect plant responses to unsuitable environmental conditions[66,67], which may help the development of tools and specific protocols for enhancing crop plant production.

Hormopriming is considered one of the most effective methods and is widely applied by seed companies to improve stress tolerance in crop plants, such as drought in maize[68], salinity in wheat[69] and chilling in rice[70]. ABA and GAs are recognized to control physiological, biochemical, and molecular mechanisms in tomato, such as germination, seedling growth, transportation and partitioning of specific nutrients, and reprogramming of gene expression, as reported by Nakaune et al.[6]. Knowledge about the dynamic changes in phytohormone and gene expression during seed priming and during germination may facilitate understanding of the biological mechanism to develop new concepts and specific technologies to improve agronomic traits. For instance, Yang et al.[22] shed light on the biological mechanism underlying rapid germination in tomato seeds treated with hormopriming, discussing the dynamic changes in the transcript levels involved in the ABA and GA pathways. The study detected higher expression levels of Sl*CYP707A2*, which is considered an important catabolic enzyme in the ABA pathway and maintains the low concentration of ABA, in seeds with rapid germination rates.

The deleterious effect of chilling and drought conditions on the germination and development of plants is, in part, because it induces the accumulation of a large amount of ROS [71–73]. Moreover, chilling and drought conditions cause reductions in carbohydrates, lipids, and proteins, resulting in cell damage. Most rice varieties are sensitive to low-temperature conditions during germination and seedling development, leading to severe economic losses [74,75]. Wang et al.[70] investigated the effects of seed hormopriming (salicylic acid) against chilling stress on rice germination and seedling growth. The results showed increasing germination performance and enhanced morphological attributes, such as length of shoots and weight of shoots, and weight of roots. In this case, the agronomic improvements were correlated with higher α-amylase activity and total soluble sugar content. In accordance with these results, Pál et al.[76] suggested a similar response to hormopriming in the enhancement of plant tolerance to chilling stress by modifying the antioxidant activity system. As a natural response to stress, priming seed methods induce higher α-amylase and/or β-amylase activity, which results in an increased breakdown of starch and subsequent buildup of sugar levels. These enzymes play pivotal roles in mitigating environmental stress by increasing the rate of respiration, improving germination speed, and promoting suitable seedling emergence and establishment in plants[77].

Exogenous application of methyl jasmonate (20 µM) and/or salicylic acid (2 mM) in maize (*Zea mays* L.) seeds showed the ability to improve physiological and biochemical attributes under drought stress in comparison to hydropriming[68]. Likewise, Samota et al.[78] primed drought-tolerant and drought-sensitive rice seeds with methyl jasmonate or salicylic acid under drought conditions. The experiment detected effective growth and development of plants because of the mitigating of damaging effects of drought stress on the plant by increasing antioxidant activities in the shoot, lowered lipid peroxidation, reduced protein oxidation, and upregulated expression of drought-responsive genes. In

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another study, exogenous hormone application (5 mM GA_3) improved the germination and establishment of alfalfa (*Medicago sativa*) seedlings under saline conditions (200 mM NaCl) by enhancing the activities of antioxidant enzymes (*CAT*, *SOD*, and APX) and reducing membrane damage[79,80].

2.5. Nanopriming

Nanotechnology is an advanced method for agriculture because it has shown promising agronomic responses for a wide range of crop plants[81,82]. Nanoparticles have demonstrated enhanced biological activity in plants via nanofertilizers[83] and reduced toxicity of nanoherbicides[84] and nanopesticides[85] in recent decades[86].

Nanopriming agents, such as silver and zinc oxide nanoparticles[87–90], have been used to enhance germination indexes and seedling establishment in several plant species: *O. sativa*[91], *Carthamus tinctorius*[92], *Citrullus lanatus*[93], and *Thymus kotschyanus*[94]. Moreover, nanopriming is one of the most efficient methods to induce salt tolerance capacity in plants by enhancing physiological and biochemical responses[95]. In this context, Shafiq et al.[96] detected improvements in agronomic traits of wheat plants treated with fullerenol nanopriming (0, 10, 40, 80 and 120 nM concentration) under salt stress (150 mM NaCl). The study showed that fullerenol induced better K^+, Ca^{2+} and P uptake, which was reflected in better ionic and ROS homeostasis and conferred grain yield recovery by plant stress resilience. Another study evaluated the germination indexes and seedling enhancement of sorghum [*S. bicolor* (L.) Moench] treated with nanoiron oxide (n-Fe_2O_3) under salt stress (150 mmol NaCl solution)[97]. The results demonstrated significant salt tolerance in plants treated with nanopriming through physiological improvements, such as photosynthetic rate, chlorophyll index, photosystem II efficiency, and relative water content, with the aim of decreasing membrane damage.

Further investigations at the molecular point of view, although scarce in nanopriming studies, would allow researchers to develop agronomic strategies to enhance crop production under stress conditions and to utilize natural resources more efficiently.

2.6. Matrix priming (MP)

In MP, seeds are mixed with organic/inorganic solid or semisolid water carriers (charcoal, clay, peat moss, sand, sawdust, vermiculite) during imbibition and incubated for a predetermined photoperiod with controlled temperature and oxygen availability[23,98,99]. In this procedure, the matrix potential of the priming solution with high water-holding capacity induces a slowdown of solute uptake by seeds, similar to the water soaking phenomenon experienced by seeds in a natural environment. Then, seeds are separated from the matrix and dried to near the initial moisture level. The procedure is flexible (by mixing with other materials), cost-effective, and able to treat a large number of seeds[100]. Important enhancement in crop production has been noted in many reports for the use of MP under environmental stress, such as drought[23], salinity[101], and low temperature[102].

In an attempt to establish a protocol for MP, a classic investigation used artificial soil media in flats under supra-optimal temperature in comparison to polyethylene glycol (8000), inorganic salts, and nontreated seeds[98]. The study detected that tomato (*L. esculentum*), carrot (*Daucus carota*) and onion (*Allium cepa*) treated with MP improved seedling

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emergence by 50% and increased the dry weight by acquiring thermotolerance compared to nontreated seeds. In another study, broccoli and cauliflower seeds were subjected to MP (vermiculite and water) for two days of incubation[101]. Salt stress (50, 100, 150 or 200 mM NaCl) was mitigated with MP treatment by increasing the physiological attributes and biochemical activity, such as peroxidase and catalase, and the contents of proline, soluble sugar, and protein in both plant species. In this case, the accumulation of proline and soluble sugar in cells, as well as the high activities of protective enzymes, aided in enhancing salinity tolerance in broccoli and cauliflower. Moreover, the great availability of O_2 to the seeds during the MP procedure may help the respiratory system, since it directly affects seed vigor[103]. In another study, Sen et al.[104] investigated the physiological and biochemical responses in mung beans (*Vigna radiata*) through MP with chitosan to overcome the adverse effects of salinity stress. Chitosan is recognized due to its biodegradability, bioactivity, biocompatibility, and nontoxicity to crop plant production. MP treatment significantly reduced the H_2O_2 and MDA content and increased the accumulation of protein, antioxidant activity, and phenolic compounds, leading to better plant growth-promoting traits.

2.7. Biopriming

Although it is not widely used in crop plant production, biopriming is an emerging, ecofriendly and promising method in which strains of *Bacillus* spp., *Enterobacter* spp., *Pseudomonas* spp., and *Trichoderma* spp., among others, are applied to seeds to improve germination indexes and uniformity, as well as seedling vigor and growth parameters[24,105]. In this method, the inoculation of beneficial microorganisms in seeds is able to colonize the rhizosphere, reducing seed and soilborne pathogens and hence improving the endophytic relationships with the plant[34,105–108]. Despite few investigations of agronomic performance[109], biopriming has shown great synergistic potential between microorganisms and plants in inducing biotic and abiotic resistance[12,110–113].

Mycorrhizal fungi have the natural potential to activate the aggregation of several important proteins and transcripts on the roots, which improves the plant defense mechanism system[114]. Rozier et al.[108] used plant growth-promoting rhizobacteria (*Azospirillum lipoferum*) in maize cultivars, which improved the germination rate and seedling defense system by stimulating biochemical and physiological activity. In another experiment with biopriming, *Trichoderma harzianum* promoted drought tolerance in wheat through physiological protective mechanisms and increased phytopathogen resistance[115]. Additionally, working with *Trichoderma* as a biopriming agent in wheat, Meena et al.[116] reported enhancements in height, root length, yield, and chlorophyll content in different soil conditions. The study detected the improvement of nitrogen use efficiency, which is considered a relevant agronomical trait, since approximately 50% of the N applied to the field in intensive agricultural production systems is lost through leaching, surface runoff, volatilization, denitrification, and microbial consumption[117,118].

Biopriming has been investigated as a disease management method because endophytic microorganisms can reduce biotic stress, which helps the biological system defend against phytopathogens[119]. In this way, Singh et al.[120] reported phytopathology control (*Rhizoctonia solani*) in maize treated with biopriming (*Pseudomonas aeruginosa*) via enhancement of antioxidative defense enzymes. A significant enhancement in

 doi:10.20944/preprints202109.0364.v1

physiological and biochemical responses was detected in maize plants treated with biopriming, such as activation of the phenylpropanoid pathway and enhanced accumulation of proline. The study also detected a significant regulation of stress-responsive genes (*PR-1* and *PR-10*). In pearl millet [*Pennisetum glaucum* (L.) R. Br], biopriming with *Pseudomonas fluorescens* improved the germination and growth indexes and promoted resistance against downy mildew disease (*Sclerospora graminicola*) by physiological changes[121].

2.8. Physical priming

2.8.1. Heat/Cold priming

Temperature stress limits crop production and threatens global food security[122,123]. Crop plants that experience unsuitable environmental temperatures at the seed germination, seedling growth, and/or vegetative stage may impact negative effects on yield productivity through a cascade of physiological, biochemical, and molecular changes[124–126]. Efficient photosynthesis and photosynthetic partitioning are required for normal plant development. Considering that photosynthesis is highly sensitive to temperature, heat stress may disrupt chloroplast structures and their specific functions, decreasing the chlorophyll amount and stimulating the loss of crop production[127].

In heat/cold priming, seeds are subjected to different temperatures for a predetermined period with minimal physiological impact. The seeds treated with heat/cold priming techniques allow activating biological mechanisms such as osmolytes and antioxidative defense, which are responsible for improving germination and plant development by reducing thermoinhibition. Heat priming is able to induce stress-responsive proteins (heat-shock proteins and late embryogenesis abundant proteins) and reprogram metabolic homeostasis and, which confers significant thermotolerance, allowing plants to withstand subsequent thermal stresses[13,128,129]. In this context, heat stress was conducive to a significant grain yield reduction in winter wheat, while heat primed seeds (40 °C for four hours) did not show such a loss of yield[130]. The study detected improvements in photosynthesis and antioxidant activity by gene expression modifications that lead to the thermotolerance of winter wheat plants. Although heat/cold priming in seeds has shown satisfactory results in crop production, most heat/cold priming investigations are made in vegetative tissues and rarely in seeds[131].

Previous reports have studied the biological mechanisms of heat/cold priming to overcome the stress induced by temperature changes[125,132,133]. Moderate temperature as a priming treatment has shown physiological improvement in relation to stress tolerance under high temperatures in *Agrostis stolonifera* L.[134]. The study suggested that heat tolerance is a natural response to the higher concentration of saturated fatty acids in the leaf membranes. In another investigation, cold priming ameliorated cold stress in chickpeas[135]. Seeds were primed at 5 °C for 30 days, and plants were raised in a controlled environment. Cold stress negatively affected the biological mechanisms of chickpea plants, such as photosynthetic ability and photoassimilation capacity, and decreased the redox status of the cells and the production of osmolytes. Cold tolerance ability was detected in primed plants at the reproductive stage, according to the authors because of the improved leaf function, such as hydration status and photosynthetic and carbon fixation ability, in comparison to plants without priming treatment. Thus, although less information is available on the biological mechanism and molecular changes in seeds subjected to heat/cold priming, this method may contribute to inducing thermotolerance in crop plants for hotspot regions of warming levels of temperature changes[136].

2.8.2. Cold plasma priming

Cold plasma is an ecofriendly and cost-effective priming method to efficiently improve crop plant production[133,137–139]. Cold plasma priming involves the application of a mixture with ionized gas, positively charged particles, electrons, and neutral gas to seeds, which stimulates biological mechanism changes, such as the density of reactive oxygen species, phytohormone catabolism, reactive nitrogen species, and electrical conductivity[139,140]. According to several authors, in addition to eliminating phytopathogen contamination, this priming process also modifies the seed surface and facilitates the seed water uptake capacity, breaking dormancy and thus triggering modifications in hormones[133], the proteome[141], secondary metabolites[142], and tissue differentiation[143], leading to fast germination and better seedling growth and improving tolerance to environmental stress[133,137,139,140,144].

In previous studies, physiological and biochemical responses were enhanced by cold plasma exposure in many crop plants: *T. aestivum* and *A. sativa*[145], *O. sativa* L.[18], *Gossypium hirsutum* L.[146], *Pisum sativum* L. and *Cucurbita pepo* L.[147]. Seed treated with cold plasma has shown long-term effects at a later stage, such as the seedling stage[133,139], to cope with biotic and abiotic stressors, such as drought stress and disease stress. For instance, Jiang et al.[137] reported that the exposure of tomato seeds to cold plasma (80 W) efficiently increased germination and growth response and regulated the defense mechanism system in the resistance to bacterial wilt (*Ralstonia solanacearum*). Similarly, Li et al.[144] reported that cold plasma treatment (120 W) in peanuts improved the germination rate, increased the shoot and root dry weights, and improved yield in comparison to the nonprimed treatment. Such improvements are related to the leaf area, nitrogen concentrations, and chlorophyll content increasing in response to cold plasma treatment. In another study, tomato seeds primed with cold plasma improved the germination potential and seedling growth rate under drought stress[133]. Moreover, the study detected improvements in antioxidant activity, phytohormone synthesis, and defense gene expression (β-1,3-glucanase) of tomato seedlings. Although cold plasma seed priming has shown promising results in crop plant production, the biological changes and their regulation in several crop plants to mitigate biotic/abiotic stress remain unclear. With the current advances in plasma technologies, future studies could focus on plasma-triggered modifications in the cellular transcription program of genes, concentrations of hormones, and proteome issues to improve the knowledge about the complex biological mechanism changes in crop plants under stress conditions.

2.9. Hybrid priming

The physiological, biochemical, and molecular responses in seeds subjected to a single priming method are considered difficult to understand in the biological system that controls biotic/abiotic stress resistance. However, understanding the plant response becomes more complex when hybrid priming (combined priming procedures) is applied to seeds[14], plants[148], or both[149] because different priming methods promote different effectiveness in plants. In this way, considering that crop plants during their lifespan are commonly exposed to several environmental conditions, such as drought, salinity, heat/cold/freezing, and/or phytopathogens, hybrid priming treatments of seeds may be effective and a desirable method to increase multiple stress tolerances in crop plants.

Hybrid priming, a method of multiple priming combined in a specific procedure, commonly acts synergistically with priming agents, promoting agronomical attribute improvements [14] through phytohormone regulation[141,150], reprogramming of gene expression[21], and changes in biological mechanisms[151]. For instance, single electrostatic field is a priming method[152] used to recover seed vigor[14] and to induce fast germination and plant growth in crop plants[16,153,154]. In this procedure, seeds are exposed to electrical current (kilovolts/centimeters) for a predetermined time, which promotes some biological changes, such as superoxide dismutase activities in onion seeds[14] and antioxidant metabolism in wheatgrass[152]. In the same way, single hydropriming is considered a relevant technique to overcome environmental stressors[33,155], as mentioned in section 2.1 (Hydropriming). Thus, while single electrostatic field and single hydropriming improve limited biological changes, hybrid priming technology allows more biological changes to crop plants. Zhao et al.[14] developed a novel hydro-electro hybrid priming (HEHP) method to recover the potential vigor of onion seeds. They subjected the seeds to hydropriming (5 h) followed by electrostatic field irradiation (10 kv/cm for 40 s), incubation and desiccation (Fig. 4).

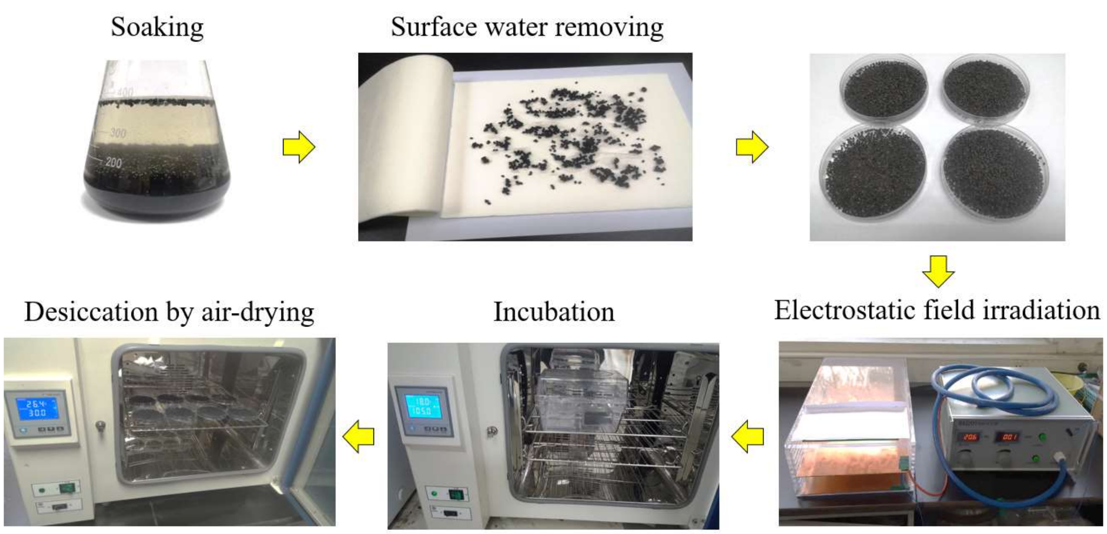

Figure 4. Hybrid priming procedure (hydro-electro hybrid priming[14]).

The combined priming method successfully recovered the potential vigor index of onion seeds (612.38) via biological mechanism changes in comparison to single hydropriming (490.26), single electrostatic field irradiation (454.85), and no priming (212.87). In the same way, our previous investigation adopted a similar HEHP method to achieve the rapid germination of tomato (*S. lycopersicum* var. HaoMei) with low vigor[156]. Potential synergism was detected between the priming procedures (hybrid priming) in phytohormone regulation (ABA/GA) and reprogramming of gene expression (Sl*NCED2* and Sl*DELLA*), which reflected the enhancement of germination indexes and vigor responses (5.09; 127) in comparison to single hydropriming (3.19; 57.42), single electrostatic field irradiation (2.47; 14,82) and no priming (2.78; 13.85). Moreover, the study detected vigor improvement of tomato seeds stored for 60 days (446.59) with HEHP samples in comparison to primed seeds without storage (127). Thus, HEHP was demonstrated to be a promising and flexible method for adaptation in other crop plants.

Compared with the efforts made to study the single priming effect to increase stress tolerance in crop plants, the biological response of plants subjected to multiple priming procedures has drawn less attention until recently, as observed by previous reports[14,157]. Hassini et al.[158] improved broccoli (*B. oleracea* L. var. Italica) sprout growth and quality under salinity stress (150 mM NaCl) by combined priming with KCl (50 mM) and methyl jasmonate. Górnik and Lahuta[151] combined 24-epibrassinolide (10^{-6}, 10^{-8} and 10^{-10} M), salicylic acid or jasmonic acid (10^{-2}, 10^{-3} and 10^{-4} M) with hydropriming (15% moisture content) followed by heat shock treatment (2 h at 45 °C) on sunflower seeds and then subjected them to chilling conditions (21 days at 0 °C) and a recovery period (72 h at 25 °C). The combined priming method increased the resistance of seedlings to chilling stress conditions mainly by promoting the activity of catalase and sugar metabolism, which alleviated the decrease in Fv/Fm. In another experiment, Li et al.[21] reported the ability of hybrid priming with exogenous salicylic acid and H_2O_2 to enhance the chilling tolerance (13 °C) of maize. Seed vigor and seedling establishment under chilling stress were improved in hybrid priming seed treatment. The synergistic effects of combined priming induced positive changes in the antioxidant system and hormone activity and increased the metabolites and energy supply, thereby providing biological conditions to enhance chilling tolerance in maize. In this case, the hybrid priming method induced the upregulation of gene expression related to GA biosynthesis, Zm*GA20ox1* and Zm*GA30ox2*, and induced the downregulation of gene expression related to GA catabolism, Zm*GA2ox1*, while ABA catabolism gene expression, Zm*CYP707A2*, and the expression of Zm*CPK11* and Zm*SnRK2.1*, encoding response receptors in the ABA signaling pathway, were all upregulated. The gene Zm*RGL2*, responsible for germination inhibition[159], was decreased in the hybrid priming treatment.

Thus, optimization and standardization of priming agents, as well as specific procedures, are required for each crop plants in the hybrid priming method according to local environmental adversity conditions to improve crop plant productivity.

3. Research Gaps and Future Perspectives

Faced with climate change, limited natural resources and the ever-increasing population around the globe, improved crop plant production with the development of new technologies that are agronomically efficient, feasible, cost-effective and, if possible, ecofriendly is urgent. Accumulated evidence has shown promising crop productivity when seeds are exposed to single or multiple priming procedures to enhance stress tolerance. Future studies with seed priming procedures may focus on the molecular level, in accordance with a proteomic and/or metabolomics approach, to identify and track the stress-responsive genes during and after priming procedures, as well as during plant development. Such studies may generate valuable results to determine the priming procedure for each plant species to enhance crop production under local adverse environmental conditions. Moreover, this work strongly encourages researchers to combine two or more priming procedures, and the use of this priming method may be valuable to synergistically activate biological mechanisms and enhance tolerance towards multiple biotic/abiotic stresses. Finally, seed companies may widely adopt priming technology as a key strategy to increase crop plant production under adverse environmental conditions.

Table 1. Synopsis of studies on seed priming procedures in the improvement of crop species productivity under stress conditions.

Crop species (scientific name/common name)	Priming procedure (rate of application)	Stress condition	Germination and seeding growth response	Crop performance and biological mechanisms change	Reference
			Hydropriming		
Helianthus annuus L. cv. Sanbro/Sunflower	Soaked (18 h at 25 °C)	Drought stress (0, -0.3, -0.6, -0.9, -1.2 MPa of osmotic potential), and salinity stress (NaCl: 0.0, 6.5, 12.7, 18.4 and 23.5 dS m^{-1} electrical conductivity)	Fast and uniform germination, low abnormal seedling percentage	Increased salt and drought tolerance, enhancement of fresh weight	Kaya et al.[33]
Lupinus angustifolius L./Lupine bean	Soaked (3 h at 20 °C)	Low temperature (7 °C) and control (13 °C)	Improved germination performance	Enhanced crop productivity via protection against low temperature damage; decreased the cell membrane permeability and ABA level	Płażek et al.[31]
Medicago truncatula var. Jemalong/Barrel medic	Soaked (2 h and 4 h)	Contaminated soil with solid waste from abandoned agricultural areas	Enhanced seed germination percentage and seedling establishment by ameliorating water uptake	Upregulation of gene expression in DNA damage repair and antioxidant defense; improved biomass	Forti et al.[34]

Moringa oleifera Lam./Moringa	Aerated water (12 h and 24 h)	Salinity levels (3, 6, 10, 14 dS m^{-1})	Enhanced moringa germination at 10 dS m^{-1} (12 h)	Improved the biomass yield, increased the chlorophyll a and b, and total phenolic content	Nouman et al.[160]
Oryza sativa/Rice	Soaked (24 h)	Flooded soil condition	Enhanced the emergence and seedling growth	Improved crop establishment, increased the rice tolerance to anaerobic conditions via maintenance of high α-amylase activity and subsequent increase in soluble sugars, and maintain lower MDA concentrations	Mondal et al.[32]
			Osmopriming		
Brassica napus L. cv. Libomir/Rapeseed	Polyethylene glycol (-1.2 MPa)	Salinity stress (NaCl:100 mM)	Improved germination and seedling growth	Enhanced salinity tolerance by up-regulation of the *P5CSA* gene, downregulation of the *PDH* gene and accumulated hydrogen peroxide contents	Kubala et al.[41]
Brassica rapa subsp. *pekinensis* cv. Lainong 50/Chinese cabbage	Urea (200 mmol/L) or KNO_3 (200 mmol/L) solution at 20 °C for 8 h	Drought stress (0, -1.0, -2.0, -3.0, -4.0, -5.0 MPa of osmotic potential)	Increased germination traits at all levels of drought stress as compared to the unprimed treatments	Priming seeds increased *CAT*, *SOD* and *POD* activity and the accumulation of proline, and soluble sugar content leading to drought tolerance enhancement	Yan[161]

Oryza sativa L. (var. Neeraja, Vaisakh and Vyttila 6)/Rice	NaCl solution (50 or 75 mM for 12 h)	Salinity stress with NaCl (75 mM - Neeraja and Vaisakh, 100 mM - Vyttila 6) and PEG (15% - Neeraja, 20% - Vaisakh and Vyttila 6)	Osmopriming showed high positive impacts on germination indexes and seedling establishment	Enhanced the stress-tolerance potential of sensitive and tolerant varieties; improved the enzymatic antioxidant contents and antioxidant enzymes activity	Sen and Puthur[162]
Sorghum bicolor (L.) Moench cv. Liao waxy No. 3/Sorghum	PEG 8000 solution (48 h at 18 °C)	Normal water supply of field capacity (25% soil moisture content), drought stress (15% soil moisture content), excessive soil moisture (35% soil moisture content)	Uniform and synchronous emergence, and decreased stress for suitable germination	Enhancement of antioxidant activities of *APX*, *CAT*, *POD*, and *SOD*; increased stress tolerance of plants under drought conditions; improved chlorophyll content and better root viability	Zhang et al.[55]
Triticum aestivum L. var. Chamran/Wheat	Potassium silicate (0, 1, 1.5 and 2 mM for 6 h); Lake Urmia saline water (0, 100, 150 and 200 mg L^{-1} of salt concentration for 10 h)	Saline water from Lake Urmia (Iran) was diluted to produce salinities with electrical conductivities (EC) of 2, 4, 6, 8, 10, 12, 14, 20 dS m^{-1}, while distilled water (EC ≈ 0 dS m^{-1}) was used for the control	Enhanced the vitality of seeds, and improved the development of seedlings	Improved salt tolerance; increased vitality index of plant development, as well as length and dry weight	Feghhenabi et al.[50]
Triticum aestivum L./Wheat	$CaCl_2$ solution (1.5% for 12 h)	Drought stress (50% field capacity)	No germination responses were recorded	Improved crop performance: leaf area, tissue water status, osmolytes accumulation and grain yield; and improved drought tolerance	Tabassum et al.[43]

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Triticum aestivum L. cv. Jimai44/Wheat	NaCl solutions (10, 30, and 50 mM)	Low-temperature stress (2 °C for 24 h)	No germination responses were recorded	Cold tolerance improvement by enhancement of photochemical efficiency; priming decreased MDA accumulation and induced cell death alleviation	Li et al.[40]
			Chemopriming		
Beta vulgaris L./Sugar beet	Tryptophan (0.0, 2.5, and 5.0 mM)	Salinity stress (320, 2000, 4000, 6000, and 8000 ppm)	No germination responses were recorded	Increased growth, yield and root quality; reduced the negative effect of salinity stress by the highest content of chlorophyll-a and chlorophyll-a/b ratio, as well as carotenoids content	Hozayn et al.[163]
Oryza sativa L. Huanghuazhan (inbred) and Yangliangyou6 (hybrid)/Rice	Selenium (50 µM)	Chilling stress (18 °C)	Improved the germination percentage	Mitigates chilling stress; triggered physiological activities, such as *SOD*, *POD*, and *CAT*, and enhanced the accumulations of glutathione and free proline; enhanced starch metabolism and high respiration rate	Hussain et al.[57]
Triticum aestivum L. cv. Kohistan-97 and cv. Pasban-90/Wheat	Sodium selenate solutions (25, 50, 75, and 100 µM for 1/2 or 1 h at 25 °C)	Drought stress	No germination responses were recorded	Increased root length, dry matter, and the biomass of plants; total sugar content and total free amino acids were enhanced	Nawaz et al.[59]

			Hormopriming		
Avena sativa L. cv. NDO-2, UPO-212 and UPO-94/Oat	Exogenous GA_3 at (100 and 150 ppm)	Salinity stress (25, 50, 75 and 100 mM of NaCl)	Improved germination and seedling growth	Enhanced shoot and root length, as well as the total fresh and dry weight, tissue water content and vigor index of plants	Chauhan et al.[164]
Cucumis sativus L./Cucumber	3-epibrassinolide (1, 5 and 10 µM)	Cadmium stress: 2.5 mM Cd solution ($CdCl_2$)	Mitigated the Cd stress during germination and seedling growth	Enhancement were detected in root fresh weight, shoot fresh weight, root dry weight and shoot dry weight; and phytohormones (auxin and ethylene biosynthesis), antioxidant activities (*SOD*, *CAT* and *APX*) and genes expression (*CS-ERS* and *C$_S$ACO1*) were higher in cucumber plants under Cd stress	Shah et al.[165]
Oryza sativa L. cv. Huanghuazhan and cv. Yangliangyou-6/Rice	Salicylic acid (100 mg L^{-1})	Chilling stress (<10 °C)	Enhanced seed germination	Increased the root length, shoot length, root fresh weight and shoot fresh weight; increased α-amylase activity and total soluble sugar contents	Wang et al.[70]
Oryza sativa L. cv. IR 20, IR 50, IR 64, ASD 16, ASD 19 and ADT 46'/Rice	Methyl salicylate (0, 25, 50, 75 and 100, mg/L)	Phytopathogen stress (*Xanthomonas oryzae*)	Increased uniform emergence and early growth stages	Enhanced root and shoot length and biomass, improved phytopathogen resistance	Kalaivani et al.[166]

Thymus vulgaris L./Thyme	Salicylic acid (100 mg L^{-1}), jasmonate (100 mg L^{-1})	Cadmium stress: 0, 10, 20, and 30 mg L^{-1}	Increased germination parameters and vigor	Increased growth attributes, as well as antioxidant enzyme activity, proline content, and reduced leaf MDA content	Moori and Ahmadi-Lahijani[67]
Triticum aestivum L. (cv. Millat-2011)/Wheat	Salicylic acid (125, 250, 375, and 500 ppm)	Salinity stress (10 dS m^{-1} NaCl solution)	No germination responses were recorded	Better starch metabolism enhanced the activities of antioxidant enzymes and reduced the lipid peroxidation rate, promoting stress tolerance and vigorous growth of plants	Hussain et al.[69]
Zea mays L. cv. CM451 NARC/Maize	Methyl jasmonate (MeJA: 20 μM) or salicylic acid (SA: 2 mM) for 18 h; combined 10 μM MeJA + 1 mM SA; hydropriming as control	Drought-induced oxidative and osmotic stress	No germination responses were recorded	Improved the physiological and biochemical attributes; increased the antioxidant enzyme activities and showed high potential to drought tolerance	Tayyab et al.[68]
			Nanopriming		
Pennisetum glaucum L./Pearl millet	Silver nanoparticles (0, 10, 20, 30 mM)	Salinity stress (0, 120 and 150 mM NaCl)	Improved germination performance	Enhanced growth attributes and antioxidant activities	Khan et al.[95]
Triticum aestivum/ Wheat	Zinc oxide nanoparticles (0, 25, 50, 75, and 100 mg L^{-1}) or iron	Cadmium stress	No germination responses were recorded	Plant traits were increased, as well as the plant productivity; enhanced photosynthesis response; reduced	Rizwan et al.[167]

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	nanoparticles (0, 5, 10, 15, and 20 mg L^{-1})			the electrolyte leakage, and enhanced the *SOD* and *POD* activities	
Zea mays L. CS-200/Maize	Titanium dioxide nanoparticles (40, 60 and 80 ppm for 24 h)	Salinity stress (200 mM NaCl)	Enhanced germination percentage and seedling vigor indexes	Mitigated the damage under salt stress conditions by enhancing antioxidant activities, improved crop development	Shah et al.[168]
			Matrix priming		
Brassica oleracea cv. No.5 Hulv and *Brassica oleracea* cv. Husong 85/Broccoli and Cauliflower	H_2O (2 days of incubation)	Salinity stress (0, 50, 100, 150 or 200 mM NaCl)	Increased the germination attributes and seedling establishment	Alleviated the salinity stress by enhancing the peroxidase and catalase activities, as well as the proline, soluble sugar and soluble protein contents	Wu et al.[101]
Vigna radiata (L.) Wilczek/Mung bean	Chitosan	Salinity stress (0 ds, 4 ds/m and 8 ds/m)	Increased the germination index	Physiological and biochemical improvements were detected in the plants; growth parameters, chlorophyll content and metabolism were increased	Sen et al.[104]
Zea mays L./Maize	Micro-Cel E (0.5g)	Chilling stress (10°C)	Increased the emergence uniformity and reduced mean emergence time	Mitigates the chilling stress; kernel density, weight, oil concentration, protein, and starch traits were improved	Hacisalihoglu et al.[169]

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			Biopriming		
Raphanus sativus L. cv. 'Antep', 'Beyaz', and 'Siyah'/Radish	*Agrobacterium rubi*, *Burkholderia gladii*, *Pseudomonas putida*, *Bacillus subtilis*, and *Bacillus megaterium* strain	Salinity stress (0, 2, 4, 6, and 8 g L^{-1} of NaCl)	Improved the germination percentage and rate	Mitigation of salinity stress was higher depending on the biopriming strain	Kaymak et al.[170]
Triticum aestivum L./Wheat	*Trichoderma harzianum* strain	Drought stress	No germination responses were recorded	Increased root vigor and shoot growth; enhanced drought tolerance by decreasing MDA and hydrogen peroxide, and an increasing in total phenolic	Shukla et al.[115]
Triticum aestivum L. cv. Sids1, cv. Stava and cv. Olivin/Wheat	Rhizosphere Bacteria	Drought stress	Enhanced the germination rate	Increased the plant parameters, biomass production and photosynthesis	Timmusk et al.[105]
Zea mays L./Maize	*Pseudomonas geniculate*	Salinity stress (150 mM of NaCl)	No germination responses were recorded	Significant increase of antioxidant enzymes, chlorophyll and carotenoids content; and increased proline content and soluble sugar	Singh et al.[126]
			Physical priming		
Brassica napus L. cv. Zhongshuang 7, cv.	Cold plasma (100 W)	Drought stress (PEG 6000)	Increased the germination rate, germination index and vigor	Drought tolerance was improved by improving antioxidant enzyme	Ling et al.[140]

Zhongshuang 11/Oilseed rape			index, and improved the dry weight of shoot and root, length of shoot and root and lateral root number of seedling	activities, increasing osmotic-adjustment products, and reducing lipid peroxidation	
Cicer arietinum L./Chickpea	Low temperature (5 °C ± 1 °C for 30 days)	Cold-stress (15/8 °C),	Pollen germination increased to 60% in relation to the control	Increased pod number and seed weight; reproductive function improved by increased the sucrose concentration in the leaves along with enhanced anti-oxidative capacity and osmo-protectants' production	Thakur et al.[135]
Solanum lycopersicum/Tomato	Cold plasma (1 min, 5 min, and 10 min)	Drought stress (PEG 6000)	Improved germination efficiency and growth of seedlings	Drought stress-tolerance potential was detected by enhancing antioxidants, phytohormone and gene expression	Adhikari et al.[133]
Solanum lycopersicum L. cv. Shanghai 906 (susceptible to bacterial wilt)/Tomato	Cold plasma (80 W)	*Ralstonia solanacearum* (bacterial wilt)	Increased both germination and plant growth	Increased the activities of antioxidant enzymes; improved the resistance to *R. solanacearum*; enhanced the dry weight of tomato	Jiang et al.[137]
Triticum aestivum L./Wheat	Cold plasma (Ar/O_2 and Ar/Air)	Cadmium contamination	No germination responses were recorded. However, the seed coat became eroded and chapped, and the pH of the	Seeds showed considerable progress in morphology and total chlorophyll synthesis; significant decrease in root and shoot Cd concentration were detected, and	Kabir et al.[171]

			seeds was significantly reduced by plasma treatment	reduced expression of Cd transporters in the root (Ta*LCT1* and Ta*HMA2*), as well as upregulation of antioxidant enzymes (*SOD* and *CAT*) were detected	
Triticum aestivum L. cv. Yangmai 16/Winter wheat	Heat-shock (40 °C for 4 h)	Heat stress (day/night temperature of 35/27 °C)	Physiological and biochemical activities improved during germination	Alleviated losses of kernel weight and grain yield by enhanced antioxidant and photosynthesis capacity; and modifications of expressions of the stress-related genes	Zhang et al.[130]
			Hybrid priming		
Brassica oleracea L. var. Italica/Broccoli	KCl (50 mM) + methyl jasmonate (25 µM)	Salinity level (150 mM NaCl)	Improved the uniform germination	Increased plant growth and counteracted salinity; provided a positive response for osmotic and water potentials, root hydraulic conductivity, and glucosinolate contents	Hassini et al.[158]
Ceratotheca triloba (Bernh.)	Smoke-water (1:500 v/v) + synthesized smoke-compound	Low temperatures (10 or 15 °C), low osmotic potential (PEG 6000 (0; -	Priming treatments stimulated germination and improved seedling grown	Alleviated abiotic stressors during seed germination and plant growth	Masondo et al.[149]

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Hook.f./Wild foxglove	karrikinolide (10^{-6} M), Kelpak® (0.4%), phloroglucinol (benzene-1,3,5-triol)	0.05; -0.15; -0.30; -0.49 MPa) and salinity stress (0; 5; 15; 25; 50 mM of NaCl)			
Helianthus annuus L. cv. Wielkopolski/Sunflower	24-epibrassinolide (10^{-6}, 10^{-8} and 10^{-10} M), salicylic acid (10^{-2}, 10^{-3} and 10^{-4} M) and jasmonic acid (10^{-2}, 10^{-3} and 10^{-4} M) followed by short-term heat shock (45 °C, 2 h)	Chilling stress	No germination responses were recorded	Reduced inhibition of roots as well as lateral roots and plants development by allowing the germinating seeds to recover from the growth-inhibiting effects of chilling; increased resistance to chilling stress via improving catalase activity and sugars metabolism	Górnik and Lahuta[151]
Silybum marianum (L.) Gaertn/Milk thistle	H_2O_2 (0, 80, 160, 240µM for 8 h) + magnetic field (0, 10, 20, 30 min)	Salinity stress (EC: 50 Ms/cm)	Increased growth of seedlings in the early stages	Increased salt-tolerance and improved physiological attributes by alleviating the oxidative damage	Migahid et al.[172]
Zea mays L./Maize	Salicylic acid (0.5 mM) + H_2O_2 (50 mM)	Chilling stress (13 °C)	Improvements in the germination indexes and seedling growth	Enhanced plant quality and plant establishment; promoted hormone metabolism and signal transduction, and enhanced energy supply and increased antioxidant enzyme activities	Li et al.[21]

Author Contributions: D.G., S.Z. and Y.Z. conceived and designed the study. D.G., S.Z., S.A. and Y.Z. wrote the manuscript. L.C.M. and D.H. wrote the manuscript and performed the critical review. All authors approved the final manuscript.

Funding: Shanghai Agriculture Applied Technology Development Program, China [Grant No. (2019) 2-3].

Acknowledgments: Special thanks are due to the Shanghai Agriculture Applied Technology Development Program for the financial support.

Conflicts of Interests: All authors declare that they have no conflict of interests, competitors and/or financial in relation to the publication of this scientific paper.

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