Seed Priming Technology as a Key Strategy to Increase Crop Plant Production under Adverse Environmental Conditions

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Abstract
Farmers and seed manufactures constantly require high-quality seeds with excellent agronomic performance. However, faced with environmental adversity, limited natural resources, and increasing food demand around the globe, 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 physio-biochemical and molecular changes, conferring specific stress tolerance to subsequent germination and growth conditions. Despite several studies that have provided positive evidence of seed priming in crop plant production, there seems less adoption of such priming on a commercial scale. In this review paper, we aimed to study the recent approaches in the efficiency of hydropriming, osmopriming, hormopriming, nanopriming, physical priming, biopriming, and novel techniques of hybrid priming procedures in the production of crop plants under environmental adversity, as well as their physio-biochemical and molecular mechanism changes. All priming methods have induced relevant changes in physio-biochemical and molecular mechanisms related to crop plant production by mitigating salinity effects, heavy metals, and flooding stress and enhancing chilling, heat, drought, and phytopathogen tolerance. Future studies using seed priming techniques may investigate molecular changes, in accordance with proteomic and/or metabolomics approaches, to identify and track stress-response genes during and after priming procedures, as well as during plant development, especially on a commercial scale. Moreover, the study strongly recommends that research combines multiple priming methods, known as hybrid priming, in their investigations to provide novel technologies and additional biological approaches in order to enhance the knowledge of crop plant science. Moreover, the use of resistant crop plant varieties/cultivars combined with priming techniques has shown efficient agronomical improvements under environmental stress conditions. Collectively, these findings shed light on the use of seed priming technology on the commercial scale as a key strategy to increase crop plant production under environmental adversity by acquiring stress tolerance and enhancing agronomic traits to meet global food demands.

Keywords: Stress Tolerance; Defense Mechanism; Biotic/Abiotic Stress; Hybrid Priming; High-Quality Seeds

Introduction
Faced with an increasing population and limited natural resources, climate change has imposed additional adverse conditions on crop plant production. This situation has worsened to the extent that food consumption, along with an increasing population, has increased disproportionately over the past few years [1]. Moreover, it is predicted that by 2050, salinization consequences will affect 50% of the world's arable land [2]. In terms of economic losses, according to the FAO, between 2005 and 2015, environmental stressors 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 [3]. At the field level, during their lifespan, 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.

Seed dormancy, among the several biological changes in crop plants that experience unsuitable environmental conditions, is considered one of the most common physiological consequences

that significantly reduce crop production [4]. Seed dormancy is characterized by the inhibition of germination while anticipating 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 techniques is seed priming [11-16]. Nevertheless, the use of resistant plant varieties/cultivars combined with priming techniques may also improve plant growth under stress conditions by enhancing the physio-biochemical and molecular system [17, 18]. Seed priming is defined as a 'pregermination' technique inducing several physio-biochemical and molecular changes, including the activation of stress-response genes associated with germination [19], in which the seed prepares for imminent environmental stress.

Stress tolerance acquired through priming treatments has been suggested to be likely 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 Figure 1.
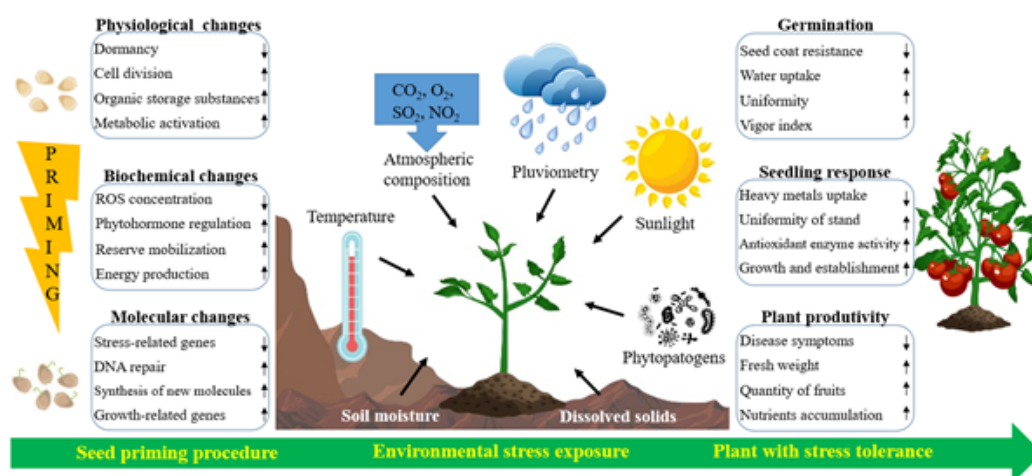

Figure 1: Schematic representation summarizing the mechanism underlying environmental stress tolerance acquired by primed seeds.

Seed priming technologies are emerging as a potential and promising method to efficiently increase crop production under adverse environmental conditions [13, 16, 20-23]. Seed priming methods are capable of improving morphophysiological patterns, regulating phytohormones, reprogramming gene expression, and inducing the metabolism of important enzymes [13, 24, 25]. Different antioxidants, such as catalase (CAT), ascorbate peroxidase (APX), superoxide dismutase (SOD), peroxidase (POD), ascorbic acid (ASH), and glutathione (GSH) are commonly triggered during seed priming procedures. Among other factors, such as turgor potential and plant water status, antioxidant enzymes protect cellular membranes against the harmful effects of reactive oxygen species (ROS) and can help mitigate environmental stressors and improve seed germination and seedling growth [26, 27].

Priming technology is appreciated by farmers and seed manufacturers due to its considerable agronomic performance with a wide range of crop plants [13, 16, 26, 28]. Several investigations have shown the advantages of seed priming procedures in crop plant production [13, 16, 20-23], and reports of the negative effects of seed priming on agriculture remain scarce [29]. However, the use of this technology is still not widely used on a commercial scale. Considering the increasing food demand, limited natural resources, and climate change, the development of agricultural strategies is urgent to produce food efficiently [16, 21, 20-23]. Considering this, the aim of this study is to summarize some of the main seed priming technologies: hydropriming, osmopriming, hormopriming, nanopriming, physical priming, biopriming, and novel hybrid priming techniques, referencing efficiency in the production of crop plants under adverse environmental conditions. Furthermore, this study provides updated progress on seed priming technology as well as the agronomical potential of physio-biochemical and molecular approaches.

Seed Priming Techniques
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 techniques subjected to stress conditions and the impact on crop plant production is listed in Table 1.

Hydropriming
Hydropriming, an eco-friendly, feasible, agronomically efficient, and cost-effective procedure to overcome environmental stress conditions, allows suitable germination and seedling growth in *Lupinus angustifolius L*, *Oryza sativa*, and *Helianthus annuus L.*

[33-35]. Hydropriming is a simple method that involves soaking seeds in pure water for a particular period at a controlled temperature under dark or light conditions [14]. Among other priming techniques, it may be considered the most used. A previous investigation reported the potential of hydropriming to enhance tolerance to low-temperature conditions in *L. angustifolius* [33]. The study investigated the impact of low temperature (7 °C) on the physio-biochemical changes during germination under the influence of the hydropriming method (3 h at 20 °C). The hydropriming procedure balanced growth regulators and enhanced the expression of transcription factors, which may improve germination efficiency. Antagonistically to ABA, GAs play a key role during germination by inducing the expression of genes encoding enzymes such as endo-β-1, 3-glucanase, β-1, 4-mannan endohydrolase, and α-amylase. These enzymes hydrolyze endosperm and suppress ABA-triggered seed dormancy [4], which may explain the enhanced germination performance in *L. angustifolius*. In this way, this study confirmed the effectiveness of hydropriming in protecting seeds of *L. angustifolius* against cold damage during germination due to reduced cell membrane permeability, regulation of amylolysis activity, and endogenous ABA levels.

Hydropriming is used to overcome irregular seed germination and stand establishment caused by adverse environmental conditions, such as drought, saline soils, and heavy-metal accumulation [36, 37]. These stressors affect cell division and hypocotyl elongation, reduce nutrient uptake and translocation, and decrease tissue water status and photosynthesis, which causes a reduction in enzymatic activity and overproduction of ROS [38]. To protect their cells from damage, plants activate a self-defense mechanism that controls ROS activities, such as H2O2 [39]. Previous works reported that genes that play roles in DNA repair are commonly used to indicate seed and seedling vigor [40, 41]. Thus, Forti et al. showed improved seed germination and seedling establishment of *Medicago truncatula* in heavy metal-contaminated soil via the seed hydropriming method [36]. The treatments upregulated genes that may have contributed to improved repair DNA damage, such as OGG1 (8-oxoguanine glycosylase) and FPG (formamidopopyrimidine-DNA glycosylase) genes. These genes are involved in base excision repair—a cellular mechanism that repairs damaged DNA throughout the cell cycle, which encodes ROS scavengers and MT2 (metallothionein type 2), both serving as a ROS scavenger and repair enzyme, respectively [42].

Another stressor, anaerobic conditions, during germination and seedling growth, normally leads to poor crop establishment and low crop yield. Mondal et al. investigated the responses of hydropriming to the growth index and physiological processes of rice during germination and seedling growth under anaerobic conditions [34]. Hydropriming significantly enhanced the emergence and seedling growth of rice in flooded soils. According to the study, hydropriming treatment improved the breakdown of stored carbohydrates by enhancing the enzymatic activities of starch catabolic enzymes, such as α-amylase, and maintained lower malondialdehyde (MDA) concentrations, as supported by other investigations [43]. MDA is considered a biomarker of oxidative damage—released during the lipid peroxidation process [44]. Thus, lower MDA activity indicates a decrease in lipid peroxidation, which maintains membrane integrity and guides primed seeds to improved germination performance. Based on most investigations, hydropriming has been found to decrease cell membrane permeability and ABA levels [33], upregulate gene expression for DNA damage repair and antioxidant defense [36], increase total phenolic content [45], reach a rapid and uniform germination [35], and improve crop establishment [15].

Osmopriming

Routinely used to enhance the vitality index of seeds, osmopriming techniques have shown promising germination and plant growth performance under several adverse environmental conditions, such as chilling, salinity, and drought [12, 46-50]. In this method, seeds are immersed in an osmotic solution with low water potential (ψ) via 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. studied osmopriming (with 1.5% $CaCl_2$ solution) in the production of wheat (*Triticum aestivum L.*) under drought stress [51]. The results revealed promising crop plant enhancement in comparison with hydropriming treatments regarding osmolyte accumulation, tissue water, leaf area, and crop yield. The positive plant responses were enhanced with osmopriming due to a considerable decrease in lipid peroxidation and acquired drought tolerance. These results are in agreement with Chen and Arora, 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 [52]. DHNs (group 2 LEA proteins) are water-soluble lipid vesicle-associated proteins involved in the adaptive responses of plants to environmental stress tolerance [53]. Later, Chen et al. improved chilling and desiccation stress tolerance in *Spinacia oleracea L.* cv. Bloomsdale by the osmopriming technique. 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 germination in response to stressors [54].

Zhang et al. investigated the physio-biochemical effects of osmopriming (PEG 8000 solution) on the germination performance and seedling establishment of sorghum (*Sorghum bicolor* (L.) Moench) under various soil moisture conditions [55]. 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, increased free amino acid contents, e.g., proline, and reduced MDA accumulation and electrolyte leakage in seedlings which led to the enhancement of drought tolerance in sorghum plants. The presence of antioxidant enzymes in plants is one of the most important factors to mitigate the harmful effects of biotic/abiotic stressors [13]. These biochemical changes in sorghum led to improved water potential in seedlings, thus offsetting the adverse effect of water stress, and provided valuable information for future studies in mitigating adverse effects in sorghum under drought stress conditions.

The low temperature recorded in wheat during the early stages of germination may disturb several physio-biochemical and molecular mechanisms and cause an imbalance between the ability of leaves to absorb light and release energy to cells in order to perform essential metabolic activities [56, 57]. Considering that there is an estimated high future demand for wheat due to an increasing world population and climate change, Li et al [48, 58]. improved the cold tolerance of wheat plants with osmopriming treatment in seeds (30 mM NaCl). The priming procedure enhanced the photochemical efficiency in seedlings by decreasing MDA accumulation and alleviating cell death. In a comparison with other priming techniques, as well in the application of hydropriming in rice (see Section Hydropriming), osmopriming was also able to maintain lower MDA concentrations, demonstrating that both priming methods are efficient in decreasing MDA activity in different plant crop species for different stressors [15].

Soil salinity is another adverse condition that causes crop plant losses, especially in arid and semiarid regions [50]. Soil salinity becomes more extensive yearly, particularly as a result of inappropriate agronomic management [59, 60]. Salinity stress conditions cause increasing osmotic pressure, ion uptake imbalances, and oxidative stress in sorghum, hence affecting early growth stages and decreasing crop production [61]. Recently, potassium silicate (K_2SiO_3) (used for osmopriming wheat seeds) was reported to be the most effective agent in comparison with spermidine, ascorbic acid, proline, and Lake Urmia saline water treatments to relieve the negative impact of salinity stress during germination and plant growth [62]. The vitality index of seeds and seedling length increased due to boosting the antioxidative defense system. Another experiment detected improvements in the germination and seedling growth of *Brassica napus* primed with polyethylene glycol (-1.2 MPa) under salinity stress (NaCl: 100 mM) [49]. According to the study, the improvement in 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 con-centrations. While H_2O_2 acts as a signaling molecule at the beginning of seed germination, involving specific changes at proteomic, transcriptomic, and hormonal levels, proline participates in the antioxidative defense system, regulating the cellular redox potential, stabilizing subcellular structures, and signaling transduction pathways that help regulate stress-response genes [63, 64]. A 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 since such molecular indicators—linked to physio-biochemical mechanism changes—allow the prediction of seed quality and may provide further knowledge to support future studies and provide assistance to seed manufacturers in order to reach a desirable commercial scale.

Hormopriming

In plant species, phytohormones naturally mediate the regulation of physio-biochemical and molecular mechanisms [4, 65]. Phytohormones, such as abscisic acid, auxin, brassinosteroids, cytokinins, ethylene, gibberellins, jasmonates, salicylic acid, and strigolactones are involved in regulating seed dormancy, germination, and plant development, as well as defense responses to environmental stressors [4, 66, 67]. These substances have been evaluated in experimental studies to detect plant responses to unsuitable environmental conditions, which may assist in developing tools and specific protocols for enhancing crop plant production [68, 69]. Hormopriming is considered one of the most effective methods and is applied to improve stress tolerance in crop plants, such as drought in maize, salinity in wheat, and chilling in rice [70-72]. In tomato, ABA and GAs are recognized to control physio-biochemical and molecular mechanisms, such as germination, seedling growth, transportation and partitioning of specific nutrients, and reprogramming of gene expression, as reported by Nakaune et al. [6].

Knowledge of the dynamic changes in phytohormone and gene expression during seed priming and during germination may facilitate an understanding of physio-biochemical and molecular mechanisms to develop new concepts and specific technologies to improve agronomic traits. For instance, Yang et al. shed light on the molecular mechanism underlying rapid germination in tomato seeds treated with hormopriming, reporting dynamic changes in the transcript levels involved in the ABA and GA pathways [24]. In the study, lower expression levels of SlCYP707A2—an important catabolic enzyme in the ABA pathway in seeds with rapid germination rates—in primed seeds were observed at the beginning of germination. Also observed in the hydropriming technique applied in *L. angustifolius*, hormopriming was effective in regulating the balance of ABA and GAs content in tomato seeds [33]. A similar result was obtained by Garcia et al. in primed tomato seeds [73]. The rapid germination performance revealed a similar pattern of phytohormone regulation (ABA and GAs) and gene expression—downregulating SlNCED2 and upregulating SlDELLA. During the tomato seed priming procedure, the key enzyme NCED is involved in ABA biosynthesis, while DELLA regulates GA responses [24]. These results are relevant for tomato-breeding programs for enhancing plant productivity.

Chilling conditions during germination and plant development cause reductions in carbohydrates, lipids, and proteins, resulting in cell damage. Most rice varieties/cultivars are sensitive to low-temperature conditions during germination and seedling development, leading to severe economic losses [74, 75]. Wang et al. investigated the effects of seed hormopriming (salicylic acid) against chilling stress on rice germination and seedling growth [72]. The results showed increasing germination performance and enhanced morphological attributes such as length of shoots, weight of shoots, and weight of roots. In this case, agronomic improvements were correlated with higher α-amylase activity, total soluble sugar content, and an improved respiration rate. As a natural response to stress, priming seed methods induce higher α-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 [76]. In another investigation, exogenous application of methyl jasmonate (20 μM) and/or salicylic acid (2 mM) in maize

(*Zea mays* L.) seeds demonstrated the ability to improve physio-biochemical attributes under drought stress in comparison to hydropriming [70]. Likewise, Samota et al. primed drought-tolerant and drought-sensitive rice seeds with methyl jasmonate or salicylic acid under drought conditions [77]. The experiment detected effective growth and development of plants due to the mitigation of damaging effects of drought stress on the plants by increasing the total phenolic content and antioxidant activities in shoots, lowering lipid peroxidation, reducing protein oxidation, and upregulating the expression of drought-response genes (*RD1* and *RD2*). Results from the use of resistant varieties/cultivars—combined with the application of plant growth regulators as elicitors of the priming procedure for activating antioxidant enzymes, regulating hormones, and stress-responsive genes—are an avenue for future studies regarding priming technology in order to overcome environmental constraints.

Nanopriming

Nanotechnology is considered an advanced method for agriculture and has shown promising agronomic responses for a wide range of crop plants [78, 79]. Furthermore, in recent decades, nanoparticles have shown enhanced biological activity in plants via nanofertilizers and reduced toxicity of nanoherbicides and nanopesticides [80-83].

Nanopriming agents, such as silver and zinc oxide nanoparticles, have been used to enhance germination indexes and seedling establishment in several plant species: *O. sativa, Carthamus tinctorius, Citrullus lanatus,* and *Thymus kotschyanus* [84-91]. Moreover, nanopriming is one of the most efficient methods for inducing salt tolerance in plants by enhancing physiological and biochemical responses [92]. In this context, Shafiq et al. 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) [93]. The study showed that fullerenol induced superior K+ uptake, which was reflected in improved ionic and ROS homeostasis and conferred grain yield recovery by plant stress resilience. Moreover, the regulation of K+ uptake contributes to improved osmotic adjustments since K+ ions act in multiple physiological processes, such as enzyme activation, membrane potential, protein synthesis, and stomata regulation [94]. Another study evaluated the germination indexes and seedling enhancement of nanoiron oxide (n-Fe_2O_3) treated sorghum under salt stress (150-mmol NaCl solution) [95]. The results indicated 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. According to the authors, these improvements may be related to the efficient penetration of nanoparticles into seeds, which leads to a higher bioavailability of iron for the physiological mechanism. Later, at the seedlings stage, the observed increase in the photosynthetic rate was likely related to enhanced chloroplast production, chloroplast size, and RuBisCO protein content and concentration [96, 97]. Successful seed priming treatment with n-Fe_2O_3 was also reported in previous studies on pearl millet, wheat, and maize [92, 98, 99]. However, further investigations at the molecular level, 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.

Physical Priming
Heat/Cold Priming

Temperature stress limits crop production and threatens global food security [100, 101]. Crop plants that experience unsuitable environmental temperatures during seed germination, seedling growth, and/or vegetative stage may have negative impacts on yield productivity through a cascade of physio-biochemical and molecular changes [102-104]. Efficient photosynthesis and photosynthetic partitioning are required for normal plant development. Considering that photosynthesis is highly sensitive to temperature, heat/cold stress may disrupt chloroplast structures and their specific functions, reducing the amount of chlorophyll and stimulating the loss of crop production[102,103,105,106]. In heat/cold priming, seeds are subjected to various temperatures for a predetermined period with minimal physiological impact. Seeds treated with heat/cold priming techniques activate physio-biochemical 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-response proteins (heat-shock proteins and late embryogenesis abundant proteins) and reprogram metabolic homeostasis, which confers significant thermotolerance, allowing plants to withstand subsequent thermal stresses [13,107,108]. Heat-shock proteins, for instance, play important physiological roles, such as functioning in innate immunity in response to environmental stressors [109]. A previous study reported that 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 yield loss [110]. Moreover, the study proved that up-regulated physio-biochemical machinery, such as antioxidant activity (SOD, POD, and CAT) and heat-shock proteins accumulation—by modifying gene expression—effectively enhanced the thermotolerance in heat-primed samples of winter wheat plants.

Cold stress adversely affects plants' physiological mechanisms, such as photosynthetic ability and photoassimilation capacity, and decreases the redox status of cells and the production of osmolytes. Previous reports have studied the physio-biochemical mechanisms of cold priming to overcome changes caused by temperature-induced stress [103,111,112]. The cold priming technique ameliorated cold stress in chickpeas [113]. Seeds were primed at 5 °C for 30 days, and plants were raised in a controlled environment. The effect of cold tolerance was detected in primed plants at the reproductive stage due to improved leaf function, such as hydration status, photosynthetic rate, carbon fixation ability, increased sucrose concentration, and better antioxidative capacity in comparison to plants without priming treatment. Efforts made with this technology would provide a suitable method for avoiding flower losses of chickpeas due to chilling temperatures. Moreover, these improvements in antioxidant activities are one of the most common biochemical responses in seeds treated with priming technology, as observed in this study, in accordance with hydropriming, osmoprimnig, hormopriming, and nanopriming [36, 114, 69, 92]. Thus, although scarce information is available on the physio-biochemical and

molecular mechanism changes in seeds subjected to heat/cold priming, this method may contribute to inducing thermotolerance in crop plants located in warm hotspot regions as a result of temperature changes.

Cold plasma priming

Cold plasma is an eco-friendly and cost-effective priming method that efficiently improves crop plant production [112,115–117]. Cold plasma priming involves the application of a mixture containing ionized gas, positively charged particles, electrons, and neutral gas to seeds, which stimulates physio-biochemical mechanism changes, such as the density of reactive oxygen species, phytohormone catabolism, reactive nitrogen species, and electrical conductivity [117,118]. According to several authors, in addition to eliminating phytopathogen contamination, this priming process also modifies the seed surface and facilitates seed water uptake capacity, breaking dormancy and thus triggers modifications to hormones, proteome, secondary metabolites, and tissue differentiation, leading to rapid germination and improved seedling growth [112, 115, 117-122].

In previous studies, physio-biochemical responses were enhanced by cold plasma exposure in many crop plants, including: *T. aestivum* and *A. sativa, O. sativa L.*, *Gossypium hirsutum L.*, *Pisum sativum* L., and *Cucurbita pepo* L. [20, 123-125]. Seeds treated with cold plasma have shown long-term effects at later stages, such as the seedling stage, to cope with biotic and abiotic stressors, such as drought stress and disease stress [112, 117]. For instance, Jiang et al. 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*) [115]. Similarly, Li et al. reported that cold plasma treatment (120 W) in peanuts improved the germination rate, increased shoot and root dry weights, and improved yield in comparison to the non-primed treatment [122]. Such improvements are related to the leaf area, nitrogen concentrations, and chlorophyll content which increase in response to cold plasma treatment. Improvement in the leaf area index is considered a relevant morpho-physiological parameter for crop yield estimation and growth status, especially since it determines the light interception capacity and light use efficiency, influencing canopy expansion and plant growth [126]. In another study, tomato seeds primed with cold plasma improved the germination potential and seedling growth rate under drought stress [112]. Moreover, the study detected improvements in antioxidant activity, phytohormone synthesis, and defense-related gene expression (*β-1,3*-glucanase) of tomato seedlings. *β*-1,3-Glucanase is recognized to play important roles in defense responses in crop plants under stress [127]. Controlling stress resistance-related genes in seeds subjected to priming techniques may generate important agronomic results that can be evaluated in other crop species.

Cold plasma seed priming has shown promising results in crop plant production, however, the physio-biochemical and molecular changes—and their regulation in several crop plants to mitigate biotic/abiotic stress—remain unclear. With current advancements in plasma technologies, future studies could focus on plasma-triggered modifications in the cellular transcription programming of genes, hormone concentrations, and proteome issues to improve knowledge of defense mechanisms in crop plants under stress conditions.

Biopriming

Although not widely used in crop plant production, biopriming is an emerging, eco-friendly, 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 [26,128]. In this method, the inoculation of beneficial microorganisms, via the seed coating process, can colonize the rhizosphere, reducing seed and soilborne pathogens and hence improve the endophytic relationships with the plant [36, 128-132]. Despite few investigations of agronomic performance, biopriming has shown great synergistic potential between microorganisms and plants in inducing biotic and abiotic resistance [12, 133-137]. Furthermore, biopriming has been investigated as a disease management method since endophytic microorganisms can reduce biotic stress, which helps the defense system against phytopathogens [138]. Recently, Singh et al. reported phytopathology control (*Rhizoctonia solani*) in maize treated with biopriming (*Pseudomonas aeruginosa*) via the enhancement of antioxidative defense enzymes. A significant enhancement in physiological and biochemical responses was detected in maize plants treated with biopriming, such as activation of the phenylpropanoid pathway. The study also detected the regulation of two stress-response genes (PR-1 and PR-10). In comparison with other priming techniques, cold plasma priming has also been used for controlling phytopathogens in tomato seeds (bacterial wilt, *R. solanacearum*; Section Cold Plasma Priming) [115].

Rozier et al. used plant growth-promoting rhizobacteria (*Azospirillum lipoferum*) in maize cultivars, which improved the germination rate and seedling defense system by stimulating physio-biochemical activity [132]. Mycorrhizal fungi have the natural ability to activate the aggregation of several important proteins and transcripts on the roots, improving a plant's defense mechanism system [140]. Growth stimulation was likely due to the accumulation of glucose content, which enables positive crosstalk with various phytohormones, such as auxins, cytokinins, gibberellins, abscisic acid, brassinosteroids, and strigolactones [141]. Regarding plant defense, the authors detected that 4-hydroxycinnamic acid, a phenolic key component in plant defense, and the microbial-specific component N-acetylglucosamine, which plays an important role in Gram-positive bacterial and fungal cell walls and Gram-negative bacterial membrane-associated lipopolysaccharides, exhibited high contents in the seeds [142, 143]. The biopriming procedure with *A. lipoferum* improved the physio-biochemical system in maize, which, according to the authors, may improve germination performance and seedling growth in plants under stress conditions. However, combining a crop cultivar with a biopriming technique, seldom reported in biopriming studies, may also aid in improving the resistance machinery system to mitigate phytopathology stress.

Meena et al., working with *T. harzianum* as a biopriming agent in wheat, reported enhancements in height, root length, yield,

and chlorophyll content in different soil types (alluvial, red, and black) and nitrogen doses (0, 30, 60, and 120 kg/ha) [144]. Nitrogen is vital since it acts directly on photosynthesis; it is also a constituent part of chlorophyll, vitamins, carbohydrates, and proteins, and acts on plant growth development. The study detected the improvement in nitrogen use efficiency in alluvial soil combined with 120 kg/ha of nitrogen followed by seed biopriming. The improvement in nitrogen use efficiency is considered a relevant agricultural trait as it alleviates environmental pollution, reduces nitrogen demand, and the final market price of vegetables—since approximately 50% of the nitrogen applied to the field in intensive agricultural production systems is lost through leaching, surface runoff, volatilization, denitrification, and microbial consumption [145, 146]. Different studies of the biopriming technique have shown improvements in the plant defense mechanism system and enhanced nitrogen use efficiency, which may be reflected in plant resistance against phytopathogens and increased crop plant production [132, 139, 144].

Drought-tolerant *Trichoderma harzianum* strains promoted drought tolerance in wheat through osmoregulation and protective physiological mechanisms [147]. L-Phenylalanine ammonia-lyase (L-PAL) is a mechanism known for improving abiotic stress tolerance via the synthesis of phenolic compounds. Enhancing the capacity to scavenge ROS and increase L -PAL activity in leaves resulted in resistance improvement to drought stress in wheat plants treated with *T. harzianum.* Thus, the use of resistant plant varieties/cultivars combined with the priming technique has already shown promising results in the stress-response activity in promoting crop production improvement; however, the use of tolerant biopriming agents is a promising field that should be further explored [35, 128, 148].

Hybrid priming

Hybrid priming is a method of multiple priming combined in a specific procedure and commonly acts synergistically with priming agents, promoting improvements in agronomical attributes through phytohormone regulation, reprogramming of gene expression, and changes in the defense system [14, 23, 119, 149, 150]. Compared with single priming techniques, the physio-biochemical and molecular response of plants subjected to hybrid priming procedures has drawn less attention until recently, as observed in previous reports [14, 151]. Understanding the plant response may generate valuable morpho-physiological, biochemical, and genetic responses when hybrid priming is applied to seeds, plants, or both since, in crop plants, different priming methods promote different extents of effectiveness [14, 152, 153]. In this way, considering that during their lifespan, crop plants 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. For instance, the single electrostatic field is a seed priming method used to recover seed vigor and induce rapid germination and plant growth in crop plants[14, 16, 154-156]. In this procedure, seeds are exposed to an electrical current (kilovolts/centimeters) for a predetermined time, which promotes physio-biochemical changes, such as superoxide dismutase activities in onion seeds and antioxidant metabolism in wheatgrass [14, 154]. In the same way, single hydropriming is considered a relevant technique for overcoming irregular seed germination and stand establishment [140]. Thus, while single electrostatic field and single hydropriming induce limited changes, hybrid priming technology affords a greater number of biological changes to crop plants. An example of this was demonstrated by Zhao et al., who developed a novel hydro-electro hybrid priming (HEHP) method to recover the potential vigor of onion seeds Figure 2 [14].
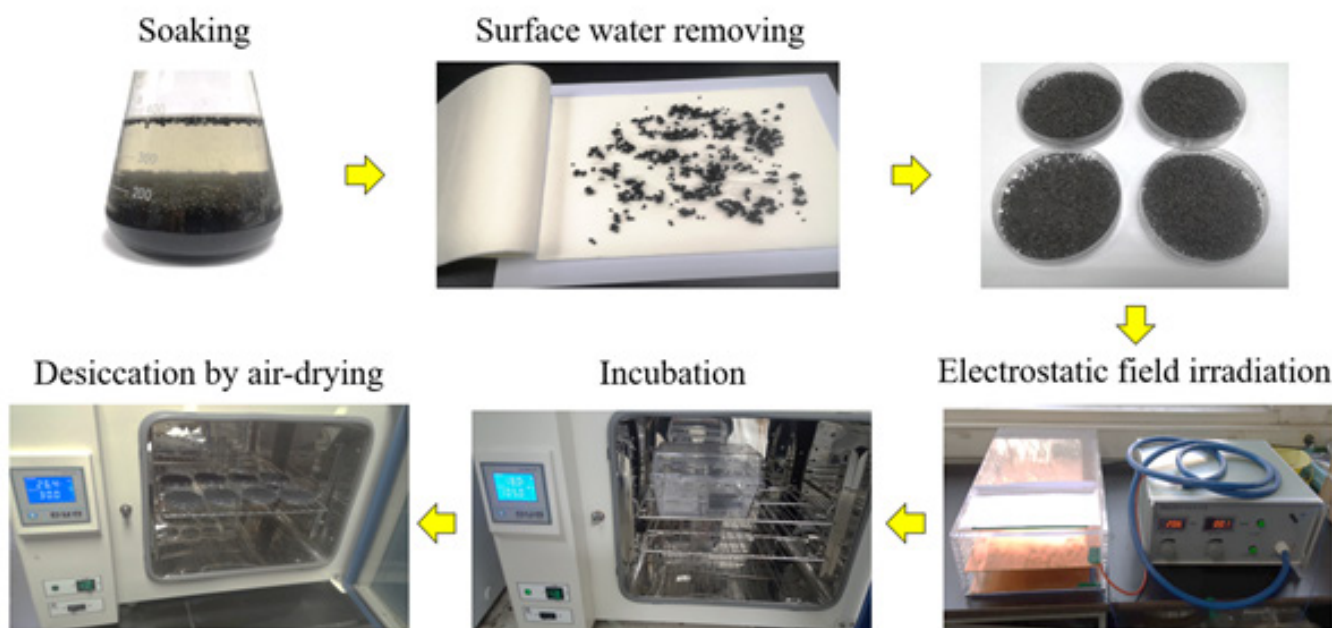

Figure 2: Hybrid priming procedure (hydro-electro hybrid priming) [14].

Seeds were subjected to hydropriming (5 h) followed by electrostatic field irradiation (10 kv/cm for 40 s), incubation, and desiccation. The combined priming method recovered the potential vigor index of onion seeds (612.38) via changes in the physio-biochemical mechanism in comparison to single hydropriming (490.26), single electrostatic field irradiation (454.85), and no priming (212.87). Likewise, a previous investigation adopted a similar HEHP method to achieve the rapid germination of tomato (*S. lycopersicum* var. HaoMei) with low vigor [73]. Potential synergism was detected between the priming procedures in relation to phytohormone regulation (ABA/GA) and reprogramming of gene expression, highlighting SlNCED2 and SlDELLA, two key genes related to dormancy/germination in tomato seeds, as detailed in Section Hormopriming [6, 24]. Synergism is understood as a combination/interaction of factors/substances that causes an overall effect that is greater than the sum of individual results [158]. This was reflected in 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 in primed seeds stored for 60 days (446.59) in comparison to primed seeds without storage (127), which may be considered a relevant result for seed manufacturers. These results corroborate a recent report that improved the germination index and vigor index of carrot (*Daucus carota* L.) with similar hybrid priming (HEHP) in comparison with hydropriming, electrostatic field, and no priming [159]. The study detected higher activity of isocitrate lyase, NAD-dependent malate dehydrogenase, pyruvate kinase, and alcohol dehydrogenase at the early stages of germination in samples subjected to HEHP. The transcriptome analysis revealed 15 critical differentially expressed genes, which encoded malate dehydrogenase, phosphoenolpyruvate carboxykinase, and pyruvate kinase. These were upregulated in HEHP treatments. Thus, HEHP was able to improve the germination index during the early stage of germination due to better-stored lipid utilization, enhanced respiratory metabolism and genes expression changes. The hybrid priming (HEHP) techniques—mentioned in the previous studies—have, among them, a potential common synergism. The combined priming methods, appropriately ordered, are: hydropriming and electrostatic field followed by the process of incubation and desiccation may boost the physio-biochemical and molecular system in comparison with single priming. This likely occurs since hybrid priming has the ability to trigger multiple proteomic and metabolomics processes that are normally activated during synergism effects [73]. Thus, these studies proved that HEHP is a promising, feasible, and flexible tool to invigorate seeds of different crop species to be adapted by seed manufacturers on a commercial scale.

Hassini et al. 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 [160]. Górnik. Moreover, Lahuta 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 followed by exposure to chilling conditions (21 days at 0 °C) and a recovery period (72 h at 25 °C) [150]. The combined priming method increased the resistance of seedlings to chilling stress conditions mainly by promoting catalase activity and sugar metabolism, which alleviated the decrease in Fv/Fm. In another experiment, Li et al. 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 [23]. The synergistic effects of combined priming induced positive changes in the antioxidant system, hormone activity, and increased 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, ZmGA20ox1 and ZmGA30ox2, and induced the downregulation of gene expression related to GA catabolism, ZmGA2ox1, while ABA catabolism gene expression, ZmCYP707A2, and the expression of ZmCPK11 and ZmSnRK2.1, encoding response receptors in the ABA signaling pathway, were all upregulated. The gene ZmRGL2, responsible for germination inhibition, was decreased in the hybrid priming treatment [161].

Thus, optimization and standardization of combined priming agents, as well as specific procedures, are required for each plant species in the hybrid priming method according to local adverse environmental conditions.

Conclusion and Future Research Needs

Accumulated evidence has demonstrated promising crop productivity when seeds are exposed to priming procedures to enhance stress tolerance. The use of resistant plant varieties/cultivars combined with priming techniques may require more studies to prove plant growth efficiency under stress conditions in comparison with non-resistant varieties/cultivars combined with priming techniques. It is suggested that future re-search—using seed priming techniques—focuses on the molecular level, in accordance with proteomic and/or metabolomics approaches, in order to identify and track stress-response genes during and after priming procedures, as well as during plant development on a commercial scale. Such studies may generate valuable results to determine an appropriate priming procedure for each plant species to enhance crop production under local adverse environmental conditions and provide new information for future investigations. Moreover, this work strongly encourages researchers to combine two or more priming procedures. The use of the hybrid priming method may be valuable to synergistically activate physio-biochemical and molecular mechanisms and enhance tolerance towards multiple biotic/abiotic stresses. Finally, seed manufacturers and farmers may widely adopt priming technology as a key strategy to increase crop plant production on a commercial scale 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 physio-bio-chemical and molecular 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.[35]
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.[33]
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.[36]
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 bio-mass yield, increased the chlorophyll a and b, and total phenolic content	Nouman et al.[162]
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.[34]
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.[49]
Brassica rapa subsp. pekinensis cv. Lainong 50/Chinese cabbage	Urea (200 mmol/L) or KNO3 (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[114]

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[163]
Sorghum bicolor (L.) Moench/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	Spermidine (0, 0.5, 1 and 1.5 mM) for 10 h; ascorbic acid (0, 50, 75 and 100 mM) for 24 h; proline (0, 12, 17 and 20 mm) for 2 days, potassium silicate (0, 1, 1.5 and 2 mM) for 6 h, or Lake Urmia saline water (0, 100, 150 and 200 mg L^{-1} salt) 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.[62]
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.[51]
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.[48]
Hormopriming					
Avena sativa L. cv. NDO-2, UPO-212 and UPO-94/Oat	Exogenous GA3 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]

Species/Common name	Priming agent	Stress	Germination effect	Other effects	Reference
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 CSACO1) were higher in cucumber plants under Cd stress	Shah et al.[99]
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.[72]
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.[165]
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[69]
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.[71]
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.[70]
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.[92]
Triticum aestivum/ Wheat	Zinc oxide nanoparticles (0, 25, 50, 75, and 100 mg L−1) or iron nanoparticles (0, 5, 10, 15, and 20 mg L−1)	Cadmium stress	No germination responses were recorded	Plant traits were increased, as well as the plant productivity; enhanced photosynthesis response; reduced the electrolyte leakage, and enhanced the SOD and POD activities	Rizwan et al.[98]

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.[166]
Physical priming					
Brassica napus L. cv. Zhongshuang 7, cv. Zhongshuang 11/ Oilseed rape	Cold plasma (100 W)	Drought stress (PEG 6000)	Increased the germination rate, germination index and vigor index, and improved the dry weight of shoot and root, length of shoot and root and lateral root number of seedling	Drought tolerance was improved by improving antioxidant enzyme activities, increasing osmotic-adjustment products, and reducing lipid peroxidation	Ling et al.[118]
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.[113]
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.[112]
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.[115]
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 was significantly reduced by plasma treatment	Seeds showed considerable progress in morphology and total chlorophyll synthesis; significant decrease in root and shoot Cd concentration were detected, and reduced expression of Cd transporters in the root (TaLCT1 and TaHMA2), as well as upregulation of antioxidant enzymes (SOD and CAT) were detected	Kabir et al.[167]

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.[110]
Biopriming					
Pennisetum glaucum (L.) R. Br cv. HB3/ Pearl millet	*Pseudomonas fluorescens*	*Sclerospora graminicola* (Sacc.) Schroet	Improved the germination index	Promoted growth indexes and resistance against downy mildew disease (Sclerospora graminicola)	Raj et al.[148]
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.[168]
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.[147]
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.[128]
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.[104]
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.[160]
Ceratotheca triloba (Bernh.) Hook.f./ Wild foxglove	Smoke-water (1:500 v/v) + synthesized smoke-compound karrikinolide (10−6 M), Kelpak® (0.4%), phloroglucinol (benzene-1,3,5-triol)	Low temperatures (10 or 15 °C), low osmotic potential (PEG 6000 (0; -0.05; -0.15; -0.30; -0.49 MPa) and salinity stress (0; 5; 15; 25; 50 mM of NaCl)	Priming treatments stimulated germination and improved seedling grown	Alleviated abiotic stressors during seed germination and plant growth	Masondo et al.[153]

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 La-huta[150]
Silybum marianum (L.) Gaertn/Milk thistle	H2O2 (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.[169]
Zea mays L./Maize	Salicylic acid (0.5 mM) + H2O2 (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.[23]

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.

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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