

Review

The Utilization of Seed Priming as a Tool to Overcome Salt and Drought Stresses: Is Still a Long Way to Go?

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Abstract: Abiotic stresses, sometimes due to dramatic environmental changes, such as sudden and heavy rainfalls, or drought, increasing temperatures or soil salinization, deeply affect the growth and yield of plants. Progress in terms of improving the abiotic stress tolerance of plants can be obtained via classical breeding and genetic engineering, which can be slow, or by practice, such as acclimation and seed priming. The latter can improve seedling performance, and it can be considered a short-term approach. Seed priming with different agents and bioprimering may offer the possibility to improve stress tolerance, even though its beneficial effect depends on crop species, dose, and time of application. The aim of this review is to highlight some of the current research trends that may ultimately lead to strategies for stress-proofing crop species. The focus is on those abiotic stresses, e.g., drought and soil salinity, that are most often associated with climate change and poor agricultural practices and those crops that are most important for human nutrition. Comments are provided on the challenges and pros and cons of this methodology.

Keywords: crops; abiotic stress tolerance; climate change; biotechnological tools; seed priming



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1. Introduction

The increasing impact of climate change is becoming a serious threat to plant biodiversity and agriculture. Plants must face sudden changes in temperature, flooding, drought, and increasing soil salinity due to poor agricultural practice. Such experiences of an ever-changing environment and adverse conditions are predominant and induce stress in plants. Their survival depends on strong countermeasures based on the onset of distinct sensing and signalling mechanisms that perceive and respond to stresses. When undergoing abiotic stress, a plethora of complex events are activated involving different levels, from the cellular to the whole-organism level. In these complicated mechanisms, major changes include transcriptional modifications and translational and post-translational changes [1–4]. Both genotypes and plant developmental stages play an important role in the effectiveness of stress responses [2], which is widely determined in terms of the genetic plasticity of a tolerant species [3]. Detailed information on how plants respond to salt and drought stress is available in the literature [1–4]. Plant responses to stress may depend on their intrinsic capability to cope with it, environmental conditions, and the availability of symbionts, as pointed out by Mason et al. [5].

The risk of a future lower food supply has raised the interest of researchers toward more sustainable agricultural methods to improve plant's tolerance against abiotic stresses, including salt and drought. The latter are among the most studied because of their heavy impact on plant growth and productivity; their deleterious effects on plant development and physiology have been reported in several papers [2,6,7]. The increasing risk for crop production means that researchers are looking for protocols and methods to set up in order to improve plant tolerance toward abiotic stresses, starting from the application of breeding and genetic engineering to acclimation and seed priming.

2. Overview and Conventional Priming Methods

Seed priming is dealing with seed treatments with the aim of improving seed germination and plant tolerance to stress. Seed germination is a critical parameter for the successful development of crops, and it is considered the test to determine cultivar tolerance to abiotic stress [7,8]. Seed priming involves prior exposure to abiotic stress, which makes a seed more resistant to future exposure to stressful conditions. The protocols are designed to improve germination rates by applying a series of different parameters during the initial stages of the process [3,8]. It has been applied successfully in counteracting salt stress in several glycophytes, such as tomato (*Solanum lycopersicum* L.) [9,10], hot pepper (*Capsicum annuum* var. *acuminatum* L.) [11,12], lettuce (*Lactuca sativa* L.) [13], maize (*Zea mays* L.) [14,15], okra (*Abelmoschus esculentus* L.) [16], pea (*Pisum sativum* L.) [17], pepper (*Capsicum annuum* L.) [18], milk thistle (*Silybum marianum* L.) [19], soybean (*Glycine max* L.) [20] and *Brassica napus* [21].

The basic steps of the protocols, carried out under controlled conditions, include the embedding of the seeds in solutions containing different priming agents (Figure 1), avoiding radicle protrusion; a desiccation step follows the first one [22,23]. A summary of the different methodologies and priming agents is reported in Figure 1.

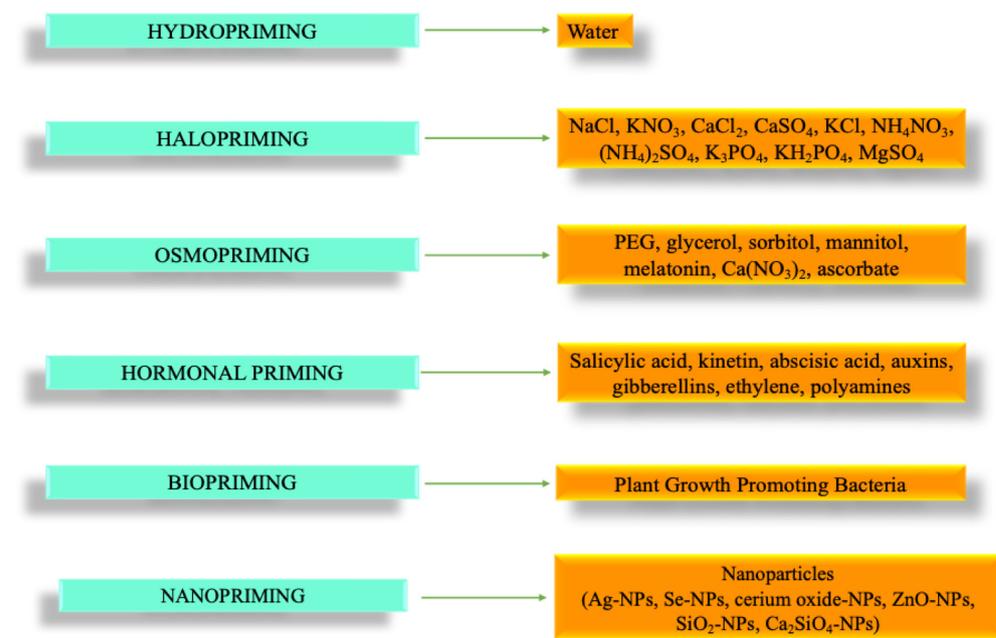


Figure 1. Protocols of priming and priming agents used in experimental practice. NaCl: sodium chloride; KNO₃: potassium nitrate; CaCl₂: calcium chloride; CaSO₄: calcium sulphate; KCl: potassium chloride; NH₄NO₃: ammonium nitrate; (NH₄)₂SO₄: ammonium sulphate; K₃PO₄: potassium phosphate; KH₂PO₄: potassium dihydrogen phosphate; MgSO₄: magnesium sulphate; PEG: polyethylene glycol; Ca(NO₃)₂: calcium nitrate; Ag-NPs: silver nanoparticles; Se-NPs: selenium nanoparticles; ZnO-NPs: Zinc oxide nanoparticles; SiO₂-NPs: silicon dioxide nanoparticles; Ca₂SiO₄-NPs: calcium silicate nanoparticles.

The treatment acts on the seed's pre-germinative metabolism, enhancing the performance of the following germination phase, i.e., an equal stage of germination and faster and uniform emergence with respect to unprimed seeds [8], and boosting seedling stress resistance at the same time [21,22,24] by responding quicker and better to stress exposure. The phenomenon is reported as "the primed state" [25]. Since the rapid germination of seeds and stand establishment are fundamental for growth and crop production in stressful environments, seed priming has proven to be beneficial for crops grown under such conditions (Table 1). In fact, priming protocols allow the primed seeds to develop and

counteract salt and drought stress by activating antioxidant response, both non-enzymatic and enzymatic, increase the synthesis of proline and other osmolytes, and decrease the negative effects on chlorophylls and photosynthesis [10,21,24]. The methodology is quite simple and low-cost; thus, it can be used by farmers to increase germination, the uniformity of plants in the field, and crop performance [26].

Table 1. A literature survey of more recent papers concerning different priming protocols. The table cited only papers published in the last 10 years (2013–2023).

Plant	Stress	Priming	Priming Agent	Growth Conditions	Limits	Reference
Wheat	Drought	Osmopriming	Ascorbic acid	Greenhouse	Lack of enzymatic analysis. No information about fruit and yield.	[27]
Wheat	Salt	Hormopriming	Gibberellin acid	Botanical Garden	Lack of enzymatic analysis.	[28]
Mountain Rye	Drought	Hormopriming	Gibberellic acid Salicylic acid	Laboratory	No information about fruit and yield. No metabolic analysis.	[29]
Rice	Salt	Hormopriming	Polyamines Gibberellin acid	Greenhouse	No enzymatic analysis. No information about fruit and yield.	[30]
Rapeseed	Salt	Osmopriming	PEG	Laboratory	No information about fruit and yield. No metabolic analysis.	[31]
Faba bean	Salt	Osmopriming	Melatonin	Laboratory	No information on yield and fruits.	[32]
Alfalfa	Drought	Osmopriming	PEG	Greenhouse	No biochemical analysis. No information about fruit and yield.	[33]
Tomato	Salt	Osmopriming	PEG	Laboratory	Lack of enzymatic analysis. No information about fruit and yield.	[34]
Wheat	Salt	Hormopriming	Abscisic acid	Greenhouse	Lack of metabolic analysis. No information about fruit and yield.	[35]
Wheat	Drought	Hormopriming	Gibberellic acid Salicylic acid	Field	No enzymatic analysis.	[36]
Wheat	Drought	Osmopriming	PEG	Experimental station	No metabolic analysis.	[37]
Tomato	Salt	Hormopriming	Salicylic acid	Growth chamber	No enzymatic analysis. No information about fruit and yield.	[38]
Maize	Salt	Halopriming Osmopriming	NaCl Sugar	Net house	Lack of metabolic and enzymatic analyses. No information about fruit and yield.	[39]
Chili pepper	Salt	Halopriming	NaCl KNO ₃	Laboratory	Growth limited only to 2 weeks.	[40]
Rapeseed	Salt	Hormopriming	Polyamines	Growth chamber	No information about fruit and yield.	[21]
Soybean	Salt	Hormopriming	Jasmonic acid	Greenhouse	No information about fruit and yield.	[41]
Maize	Drought	Halopriming	NaCl	Growth chamber	No biochemical analysis.	[42]
Rice	Salt	Halopriming	NaCl KNO ₃ CaCl ₂ KCl	Greenhouse	No information about fruit and yield. Lack of enzymatic analysis.	[43]
<i>Hibiscus</i> tea	Light Temperature Salinity	Halopriming	NaCl	Laboratory	Tests performed exclusively on seeds.	[44]
Winter savory	Drought	Osmopriming	PEG	Laboratory	Tests performed exclusively on seeds.	[45]
<i>Trigonella foenum-graecum</i>	Drought	Nanopriming	Magnetite nanoparticles from leaves of <i>Pulmonaria longifolia</i>	Growth chamber	Lack of metabolic and enzymatic analyses. No information about fruit and yield.	[46]
<i>Quinoa</i>	Salt	Halopriming	NaCl	Greenhouse	No information about fruit and yield. No enzymatic analysis.	[47]
Tomato	Salt	Hormopriming	Polyamines	Greenhouse	No information about fruit and yield.	[10]

According to the literature, through seed priming, abiotic stress tolerance may be obtained through the use of two strategies: (1) stimulation of the metabolic processes in the pre-germination phase related to the early mobilization of the seed storage reserve, elongation of embryo cell and endosperm weakening, i.e., conversion from quiescent seed in germinating state, and thus, increased germination [48–54]; (2) by imposing biotic stresses on seeds, which represses the protrusion of the radicle but supports stress responses, inducing cross-tolerance to abiotic stresses, the activation of enzymes, and osmotic adjustment. These stress tolerance strategies form a “priming memory” in germinating primed seeds that can play an important role in subsequent stress exposure and mediate more stress tolerance [24].

Several priming agents have been used to treat seeds [26], and, depending on the agents, different protocols are reported in the literature (Figure 1). The efficacy of the treatment is influenced by the osmotic potential of the priming solution, treatment duration, ambient temperature, seed lot and vigor, plant species, and storage conditions of the treated seeds. Thus, the effectiveness in improving stress response is variable. So far, the methods empirically applied by seed technologists require time-consuming experiments to detect and set up the best protocol [21,55].

3. Advanced Methods: Biopriming and Nanopriming

Besides chemical priming, the primed state can also be obtained through the colonization of plant roots by beneficial micro-organisms that can become endophytes [2,56,57]. Different species of Plant-Growth-Promoting Bacteria (PGPB), also reported as Plant-Growth-Promoting Rhizobacteria (PGPR), are often utilized as biofertilizers. Studies have reported improved plant fitness against environmental stress when seeds are inoculated with PGPB [2,58,59] (Table 2).

Table 2. Biopriming application to different crop species: positive effects induced by Plant-Growth-Promoting Bacteria (PGPB) on plant salt/drought responses. The entries in this table are grouped according to the oldest paper listed first. Papers published in the last 10 years (2013–2023) have been considered.

Plant	Bacteria	Stress	Conditions	Limits	Reference
Wheat	<i>Hallobacillus</i> sp., <i>Bacillus halodenitrificans</i>	Salt	Laboratory	Lack of metabolic and enzymatic analysis. No information about fruit and yield.	[60]
Chickpea	<i>Mesorhizobium ciceri</i>	Salt	Growth chamber	Lack of metabolic and enzymatic analysis. No information about fruit and yield.	[61]
Mung bean Bean Peanut	<i>Bradyrhizobium</i> sp., <i>Enterobacter</i> sp., <i>Chryseobacterium</i> sp.	Salt Drought	Growth chamber	Lack of metabolic and enzymatic analysis. No information about fruit and yield.	[62]
Mung bean	<i>Pseudomonas</i> , <i>Rhizobium</i>	Salt	Growth chamber	Lack of metabolic and enzymatic analysis. No information about fruit and yield.	[63]
Cotton	<i>Klebsiella oxytoca</i>	Salt	Greenhouse	Lack of enzymatic analysis. No information about fruit and yield.	[64]
Pepper	<i>Bacillus licheniformis</i>	Drought	Growth chamber	Lack of enzymatic analysis. No information about fruit and yield.	[65]
Wheat	<i>Serratia</i> spp., <i>Aerococcus</i> spp.	Drought	Jars with soil	Lack of metabolic and enzymatic analysis. No information about fruit and yield.	[66]
Mung bean	<i>Rhizobium</i> sp., PGPR	Salt	Field	Lack of enzymatic analysis.	[67]
Rice	<i>Bacillus pumilus</i> , <i>Pseudomonas pseudoalcaligenes</i>	Salt	Greenhouse	No information about fruit and yield.	[68]
Wheat	<i>Azospirillum lipoferum</i> , <i>Pseudomonas fluorescens</i>	Salt	Greenhouse	Lack of enzymatic analysis. No information about fruit and yield.	[69]
Rice	<i>Bacillus amyloliquefaciens</i>	Salt	Greenhouse	Lack of enzymatic analysis. No information about fruit and yield.	[70]

Table 2. Cont.

Plant	Bacteria	Stress	Conditions	Limits	Reference
Rice	<i>Serratia</i> sp.	Salt	Greenhouse	Lack of metabolic and enzymatic analysis. No information about fruit and yield.	[71]
Sunflower	<i>Pseudomonasaeruginosa</i>	Salt	Growth chamber	Lack of metabolic and enzymatic analysis. No information about fruit and yield.	[72]
Wheat	<i>Bacillus thuringiensis</i>	Drought	Growth chamber	No information about fruit and yield.	[73]
Maize	<i>Pseudomonas syringae</i> , <i>Pseudomonas fluorescens</i>	Drought, salt	Field	Lack of metabolic and enzymatic analysis. No information about fruit and yield.	[74]
<i>Limonium sinense</i> (Girard) Kuntze	<i>Bacillus</i> <i>Arthrobacter</i> <i>Streptomyces</i> <i>Isopterocola</i>	Salt	Greenhouse	Lack of enzymatic analysis. No information about fruit and yield.	[75]
Tomato <i>Arabidopsis</i>	<i>Enterobacter</i> sp. EJ01	Salt	Growth chamber	Lack of metabolic analysis. No information about fruit and yield.	[76]
Tomato	<i>Pseudomonasputida</i>	Salt	Greenhouse	Lack of enzymatic analysis. No information about fruit and yield.	[77]
Tomato	<i>Pseudomonas fluorescens</i> <i>Pseudomonas migulae</i>	Salt	Greenhouse	Lack of enzymatic analysis.	[56]
Cotton	<i>Pseudomonas putida</i> <i>Pseudomonas chlororaphis</i>	Salt	Growth chamber	Lack of enzymatic and metabolic analysis. No information about fruit and yield.	[78]
<i>Arabidopsis thaliana</i>	<i>Micrococcus yunnanensis</i> , <i>Paenibacillus barengoltzii</i>	Salt Drought	Growth chamber	Lack of enzymatic and metabolic analysis.	[79]
Groundnut	<i>Bacillus cereus</i> SVSCD1	Salt	Controlled conditions	Lack of enzymatic analysis. No information about fruit and yield.	[80]
Cucumber Lettuce	<i>Aspergillus niger</i> MJ1 <i>Pseudomonas stutzeri</i> DSM4166 <i>Pseudomonas fluorescens</i> CHA0-nif	Salt	Field	Lack of metabolic and enzymatic analysis.	[81]
Rice	<i>Pseudomonasstutzeri</i>	Salt	Growth chamber	Lack enzymatic analysis. No information about fruit and yield.	[82]
Velvet bean	Rhizobacteria	Drought	Growth chamber	Lack of metabolic and enzymatic analysis. No information about fruit and yield.	[83]
Sunflower	PGPB	Salt	Greenhouse	Lack of metabolic and enzymatic analysis.	[84]
Canola	<i>Brevibacterium epidermidis</i> <i>Bacillus aryabhatai</i>	Salt	Laboratory	Tests performed on seeds.	[85]
Chinese cabbage	<i>Herbaspirillum</i> sp.	Salt	Growth chamber	Lack of enzymatic analysis. No information about fruit and yield.	[86]
Chickpea	<i>Bacillus amyloliquefaciens</i> <i>Pseudomonas putida</i>	Drought	Greenhouse	Lack of metabolic analysis. No information about fruit and yield.	[87]
Rice	<i>Bacillus amyloliquefaciens</i>	Salt	Growth chamber	Lack of enzymatic analysis. No information about fruit and yield.	[88]
Paddy plants	<i>Curtobacterium albidum</i>	Salt	Greenhouse	No information about fruit and yield.	[89]
<i>Arabidopsis</i>	<i>Flavobacterium crocinum</i> HYN0056 ^T	Salt Drought	Controlled-environment chamber	Lack of metabolic and enzymatic analysis.	[90]
<i>Triticum aestivum</i>	<i>Paenibacillus pabuli</i> <i>Pseudomonas nitroreducens</i> <i>Bacillus megaterium</i>	Salt	Growth chamber	Lack of metabolic and enzymatic analysis. No information about fruit and yield.	[91]
<i>Brassica napus</i>	<i>Azospirillum brasilense</i> <i>Arthrobacter globiformis</i> <i>Burkholderia ambifaria</i> <i>Herbaspirillum seropedicae</i> <i>Pseudomonas</i> sp.	Salt	Growth chamber	No information about fruit and yield.	[58]
<i>Brassica napus</i>	<i>Arthrobacter globiformis</i>	Salt	Growth chamber	No information about fruit and yield.	[59]
Maize	Novel Bacterial Strain SH-6	Drought	Laboratory	Lack of metabolic analysis and enzymatic analysis. No information about fruit and yield.	[92]

The phenomenon of ameliorating plant growth through the use of PGPB has been known for many years, and more recent evidence has proved that enhanced defense

responses, induced by biopriming as a result of plant–plant communication in nature, can also boost crop resistance to both biotic and abiotic stresses in the field [2,93]. Researchers evidenced and appreciated the significant role played by the different bacterial species on both plant health and disease management based on their metabolic characteristics, such as the secretion of metabolites and enzymatic activity acting on plant development and response to biotic and abiotic stress [2,94,95]. Similar to rhizospheric bacteria, endophytic PGPB employ mechanisms enabling plant growth and imparting stress tolerance [57]. Thus, PGPB can help plants cope/overcome the deleterious effects of salt and drought through different interconnected mechanisms.

Some of the bacterial mechanisms involved in plant interactions have been elucidated, e.g., possible alteration of plant gene expression, thus the plant would less succumb to stress, or the bacteria ACC deaminase activity that decreases the level of stress ethylene synthesis in plant [96], or the production of different molecules, such as hormones, trehalose, proline, and betaine [2]. Moreover, the synthesis of biopolymers by bacteria as extracellular polymeric substances (EPS), like polysaccharides, may contribute to alleviating salt stress by linking Na^+ cation, thus decreasing its bioavailability [57]. Furthermore, bacteria inoculation increases the antioxidant activity of the plant and the repair of membranes. In fact, in inoculated plants, the enhanced synthesis of phenolic compounds and/or the activity of antioxidant enzymes, e.g., SOD, CAT or APX, that can detoxify reactive oxygen species, have been reported [58,59,70]. Thus, many researchers have focused their attention on strain selection and utilization as bioinoculants on plants to ameliorate their tolerance to drought and salinity stresses [2,58,97]. For this purpose, halotolerant strains have been isolated, and their plant-growth-promoting activities have been characterized [98]. The principal effects of seed priming on plants are summarized in Figure 2.

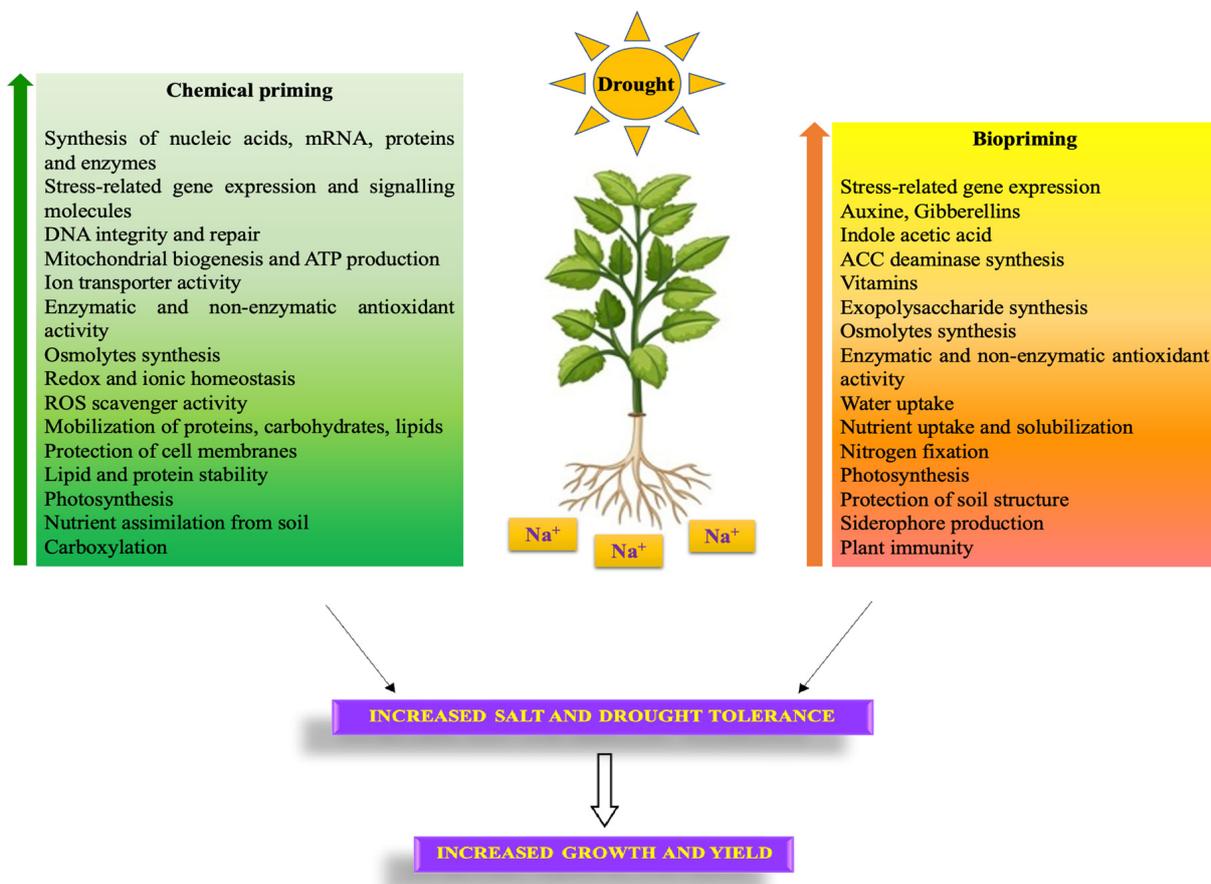


Figure 2. Overview of the positive effects of chemical priming and biopriming.

More recently, other biotechnological tools have been applied to seed priming, such as nanopriming, which uses nanoparticles (NPs) to increase plant tolerance to various types of stress [99]. Some of them can act as stimulants, i.e., can break seed dormancy and improve seed metabolism, seedling vigor and plant growth [100,101] and, in the meantime, can activate enzymatic and non-enzymatic antioxidant responses, thus stimulating plant defence systems to environmental stresses [99]. The physical–chemical properties of NPs (i.e., size, zeta potential, and concentration) are the key factors influencing their uptake and translocation within the plant, thus determining the biological responses [100,102,103]. The most common applications of NPs include, besides nanopriming of seeds, foliar application and mixing of NPs in the soil. NPs, absorbed by the seed, promote water uptake and increase the germination rate. They can also induce oxidative respiration, producing H₂O₂, a signalling molecule that activates metabolic pathways associated with seed germination, including increased α -amylase activity and gibberellin biosynthesis. Elevated H₂O₂ production activates the antioxidant defence system. Foliar and soil applications of NPs also enhance plant growth through the same signalling mechanism involving H₂O₂, improving plant productivity and tolerance under stress conditions [99].

These studies are still in their infancy; therefore, further research is needed to better understand the effects of nanotechnology and to explore the full potential of nanopriming. Moreover, in agreement with Raza et al. [99], the risks and constraints associated with the use of NPs in agriculture, should be carefully assessed by considering several factors, such as the environmental influence of their application, economic sustainability, and functional performance.

4. Salt and Drought Stress Memory

In plants, the establishment of a “memory” of a past stress event has been reported by different authors; this would provide a more rapid reaction to recurrent stress in plants being previously exposed to stress [104]. An example is provided by Sadhukhan et al. [105] in their paper: plants exposed to drought develop both short-term and transgenerational memory in terms of stress, leading to a better response to subsequent exposure to drought. Several dehydration/rehydration cycles improved the water retention of *Arabidopsis thaliana* and *Zea mays* plants with respect to plants experiencing a first stress [106–108]. According to these results, we may hypothesize that once physiological, biochemical, and molecular mechanisms have been switched on, this fact ensures enhanced protection against new stress without “costs” for the plants, being associated with constitutive expression of stress-related genes [109]. Even though there is a general claim about a positive relationship between memory and better performance, this is not always the case. In fact, we need to point out that it has been reported a negative effect of memory that may enable disruptive effects on plant performance [110] since repeated stresses provoked an increase in sensitivity toward their deleterious effects [111,112]. Based on such controversial reports, it is not possible to draw an unambiguous conclusion, and thus further studies are needed.

Another important cue concerns the duration of the memory, which can vary noticeably. It may contribute to environmental acclimation, which is considered plastic and reversible and plays a role in improving stress response [113]. Memory duration can last from days to weeks or months, and when, stable and based on epigenetic mechanisms, even extended to the offspring, which is reported as transgenerational memory [110,114]. It is noteworthy to point out that following a recurrent stimulus, opposite behaviors can be observed, either a negative lowering response, known by the term “familiarization” or habituation [115] or a positive reinforcing response, named “sensitization” [116].

The principle of priming is based on endowing “memory” of past stress events. How can priming treatment establish a memory? According to Galviz et al. [110], plant memory can be established by three possible pathways: one straightforward, which develops almost immediately without dependency on previous stimulus, and the other two based on learning and storing/calling. The three pathways can be independent or share certain connections [110]. The duration of a memory induced by priming is still a matter of debate.

So far, the known mechanisms underpinning the processes of plant memory are related to alterations in the concentration of many signalling molecules and transcription factors; those changes perfectly explain the alteration of the metabolism and the maintenance of such changes, even when stress exposure is ended and the response is obtained with recurrent exposure to stresses [114]. In their work, Conrath et al. [116] described the mechanism behind the first stress trigger accumulation or post-translational modification of single or multiple signalling proteins, which, after this event, remain inactive. Nevertheless, their presence allows an enhanced response when the plant is triggered by a second exposure to stress through hyperactivation of the signalling protein. This enhanced response is reported as cross-stress tolerance [117]. In such reversible post-translational modifications of inactive proteins that become active and vice-versa, a key role is played by phosphorylation and dephosphorylation due to the activity of members of mitogen-activated protein kinases (MAPK) [118]. It is noteworthy to mention that according to the data of several authors, the cross-stress tolerance gained towards a single stressor can lead to the tolerance of multiple stresses [119–123].

Transcriptomic research has led to the identification of changes in gene expression, levels of proteins and metabolites important in memory response [116]. From further experimental works, where the transcriptional responses to stress factors have been investigated, we have the availability of molecular data concerning memory. Several researchers have reported data on the mechanisms at the basis of the phenomenon, describing epigenetic regulation, transcriptional priming, primed conformation of proteins and other specific changes [105]. Chromatin seems to be a potential major component of the “memory” in responses to recurrent stresses, i.e., when transcription of genes, which are induced by dehydration stress, are super-induced by subsequent stress, we can observe a model for “positive memory” [104]. However, controversy still exists in the literature since the role of chromatin in transcriptional response to stress appears to be quite complex and associated with genes and stress signals and species-specific [8]. Even though we know that, for example, in drought stress, epigenetic mechanisms (e.g., DNA methylations, histone modifications and chromatin structure alterations) are important in the regulation of gene expression, contributing to epigenetic inheritance in plants transmitted to the next generation [123].

More recent data describe the effects of recurrent periods of droughts, more common than a single drought in the environment, with intermittent moist recovery intervals. While, during the first exposure to drought, plants cannot avoid the detrimental effects of the stress on plant morphology and physiology, surviving plants would memorize the first drought and respond better to the following droughts. The better response is based on a partial stomatal opening in the watered recovery interval, higher contents of osmoprotectants and ABA, and attenuation of photosynthesis in the subsequent exposure [105]. The study has demonstrated the regulating role of ABA and other hormone signalling related to transcriptional memory behavior at gene levels; high levels of histone methylation have also been reported. Interestingly, during drought, stalled RNA polymerase is detected and activated by a pause, breaking factors in a subsequent drought episode. It has been reported that during drought, DNA demethylation occurs near drought-responsive genes, with genetic control of the process. The progenies of such exposed plants show a better adaptation to this stress owing to the inheritance of such methylation patterns. Nevertheless, when the water recovery period is prolonged, it is possible to detect the loss of drought memory. These studies deserve more future research to shed more light on the genetic control of drought memory and the genetic and epigenetic controls of inheritance.

5. Application of Seed Priming Protocols to Crop Species and the Application in Agriculture

Plant response to stress depends on several factors, such as intrinsic capability to cope with a specific stress and habitat conditions. In recent years, priming-inducing activity in plants has been reported for many synthetic and natural molecules (e.g., pro-

line, L-tryptophan, glutathione, and citric acid) and secondary metabolites (e.g., polyols, ascorbic acid, lipoic acid, glycine betaine, α -tocopherol, and melatonin) [124–126]. Based on these, we have at our disposal a plethora of different protocols to mainly apply to herbaceous crops.

We have reviewed the more recent literature reporting data on seed priming applied to improve crop species tolerance to drought and salt stresses (Table 1). Recent papers on bioprimering have also been reviewed (Table 2). Both methodologies have proven to be effective, and primed plants show better performance than unprimed ones when exposed to stress conditions. The choice of priming agents depends on the species and even on the genotype; thus, careful experimental trials are required before choosing not only the best agent but also the concentration and timing of the treatment. This may be a hindrance to the wide application of the methodology, but, on the other hand, it is relatively easy to implement in the short term with respect to the required time of the other approaches. Most of the papers, beside the effects on the threshold of tolerance toward salt and drought stresses have also considered the antioxidant activities and the presence of osmolytes in the primed plants, providing an insight into the mechanisms involved in enhancing tolerance. So far, most of the studies reported results obtained under laboratory or greenhouse conditions and on the first stages of plant development and no information on fruits and yield. The field performance of primed plants is mostly lacking since only few papers report field experiments. Moreover, experiments on priming duration should be performed to ensure the durability of the treatment.

6. Conclusions

Seed priming provides a useful tool in terms of ameliorating plant response to stress. The priming methodology is easy, and the cost–benefit ratio is in favor of broad application in agriculture. Literature surveys allow us to detect an increasing number of publications dealing with this methodology and stress response in crop plants. However, the potential of seed priming has still not been fully exploited.

So far, we know that plants share common physiological and biochemical responses to stress based on the induction of gene expression involving a profound metabolic remodeling. The majority of genes are those related to defense response, involving antioxidants, osmoprotectants and polyamines, as reported in several papers.

The elucidation of the molecular mechanisms involved in priming events is an active area of research, which pinpoints common and specific biochemical traits characterizing the primed state across species. Based on the results obtained so far, it is important to underline that the technologies based on plant stress memory, cross-stress tolerance and seed priming can be important and promising areas for future research and application in agricultural science. However, our limited knowledge of the molecular dynamics of pre-germinative seed metabolism is the main hindrance to more effective new-generation techniques [127]. Successful priming protocols result from the ability to properly act on the pre-germinative seed metabolism and stimulate events that are crucial for seed quality. Nevertheless, the technique requires constant optimization, and researchers are committed to addressing some open key questions to overcome the drawbacks still present. Primed seeds show faster and more uniform germination and an improved antioxidant defence system than non-primed seeds, but the priming remains strongly influenced by various factors, such as temperature, aeration, light, priming duration and seed characteristics. As an example, Zulfiqar and co-authors [126] reported 20 chemical priming agents enabling plant tolerance to salt stress; they were categorized into different groups, such as plant growth regulators, reactive agents, osmoprotectants, vitamins, mineral elements, and polymers. These different categories explain in part the difficulties in finding a unique mechanism of action and the high variability of stress response discussed above. The application of NPs at different stages of plant development may represent a further tool in the fight against abiotic stress, but their feasibility still needs more research under the perspectives of practical usability, environmental impact, and cost-efficiency.

Anyway, the disadvantages of priming are very limited, with very few reports on the demerits of seed priming. The disadvantages do not often concern the method itself but are related to the subsequent agricultural practice: direct sowing of primed seeds is impossible, as wet seeds get caught in the seed drill, unsafe due to rain that delays sowing, or inaccessible for small farms. The benefits obtained by priming seeds may also be lost during the drying phase. Rapid drying can affect the sugar content, reducing drought tolerance and seed longevity. Sugars and their derivatives increase the desiccation tolerance and longevity of seeds, as they are involved in the maintenance and stability of glycolipids and glycoproteins of membranes during desiccation. However, during hydration, sugars are the first macromolecules to be metabolized, and the lack of subsequent re-accumulation is responsible for an accelerated deterioration.

Furthermore, most of the studies have been performed under controlled conditions, detecting the changes during the first stage of growth; to improve the effectiveness of priming and to increase the spread of this application, researchers need to make the leap from greenhouse and growth chamber to field, where the environmental conditions may influence plant responses. As reported in Tables 1 and 2, data on yield of primed plants are still lacking. In addition, among the different questions to be answered, is a question concerning the duration of the priming memory. So far, we have no or few data about the epigenetic effects of priming on the next generation. The latter will likely provide a firm basis for developing reliable tools to enhance plant health and growth in varying field conditions, such as drought and soil salinity.

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References

1. Javaid, M.H.; Khan, A.R.; Salam, A.; Neelam, A.; Azhar, W.; Ulhassan, Z.; Gan, Y. Exploring the Adaptive Responses of Plants to Abiotic Stresses Using Transcriptome Data. *Agriculture* **2022**, *12*, 211. [[CrossRef](#)]
2. Forni, C.; Duca, D.; Glick, B.R. Mechanisms of plant response to salt and drought stress and their alteration by rhizobacteria. *Plant Soil* **2017**, *410*, 335–356. [[CrossRef](#)]
3. Raza, A.; Tabassum, J.; Zeeshan Fakhar, A.; Sharif, R.; Chen, H.; Zhang, C.; Ju, L.; Fotopoulos, V.; Siddique, K.H.M.; Singh, R.K.; et al. Smart reprogramming of plants against salinity stress using modern biotechnological tools. *Crit. Rev. Biotech.* **2022**, *15*, 1035–1062. [[CrossRef](#)]
4. Athar, H.U.R.; Zulfiqar, F.; Moosa, A.; Ashraf, M.; Zafar, Z.U.; Zhang, L.; Ahmed, N.; Kalaji, H.M.; Nafees, M.; Hossain, M.A.; et al. Salt stress proteins in plants: An overview. *Front. Plant Sci.* **2022**, *13*, 999058. [[CrossRef](#)]
5. Mason, C.J.; Jones, A.G.; Felton, G.W. Co-option of microbial associates by insects and their impact on plant-herbivore interactions. *Plant. Cell Environ.* **2019**, *42*, 1078–1086. [[CrossRef](#)]
6. Bartels, D.; Sunkar, R. Drought and salt tolerance in plants. *Crit. Rev. Plant. Sci.* **2005**, *24*, 23–28. [[CrossRef](#)]
7. Lei, C.; Bagavathiannan, M.; Wang, H.; Sharpe, S.M.; Meng, W.; Yu, J. Osmopriming with Polyethylene Glycol (PEG) for Abiotic Stress Tolerance in Germinating Crop Seeds: A Review. *Agronomy* **2021**, *11*, 2194. [[CrossRef](#)]
8. Gianella, M.; Pagano, A.; Forti, C.; Guzzon, F.; Mondoni, A.; de Sousa Araújo, S.; Macovei, A.; Balestrazzi, A. Chapter 6—Molecular aspects of seed priming as a means of progress in crop improvement. In *Advances in Crop Improvement Techniques*; Woodhead Publishing: Sawston, UK, 2020; pp. 89–100.
9. Pradhan, N.; Prakash, P.; Tiwari, S.K.; Manimurugan, C.; Sharma, R.P.; Singh, P.M. Osmopriming of tomato genotypes with polyethylene glycol 6000 induces tolerance to salinity stress. *Trends Biosci.* **2014**, *7*, 4412–4417.
10. Borromeo, I.; Domenici, F.; Del Gallo, M.; Forni, C. Role of Polyamines in the Response to Salt Stress of Tomato. *Plants* **2023**, *12*, 1855. [[CrossRef](#)]

11. Khan, H.A.; Ayub, C.M.; Pervez, M.A.; Bilal, R.M.; Shahid, M.A.; Ziaf, K. Effect of seed priming with NaCl on salinity tolerance of hot pepper (*Capsicum annuum* L.) at seedling stage. *Soil Environ.* **2009**, *28*, 81–87.
12. Khan, H.A.; Pervez, M.A.; Ayub, C.M.; Ziaf, K.; Balal, R.M.; Shahid, M.A.; Akhtar, N. Hormonal priming alleviates salt stress in hot pepper (*Capsicum annuum* L.). *Soil Environ.* **2009**, *28*, 130–135.
13. Nasri, N.; Kaddour, R.; Mahmoudi, H.; Baatour, O.; Bouraoui, N.; Lachaâl, M. The effect of osmopriming on germination, seedling growth and phosphatase activities of lettuce under saline condition. *Afr. J. Biotechnol.* **2011**, *10*, 14366–14372. [[CrossRef](#)]
14. Abraha, B.; Yohannes, G. The role of seed priming in improving seedling growth of maize (*Zea mays* L.) under salt stress at field conditions. *Agric. Sci.* **2013**, *4*, 666–672. [[CrossRef](#)]
15. Tabatabaei, S. The effect of priming on germination indexes and seed reserve utilization of maize seeds under salinity stress. *Seed Res. (J. Seed Sci. Technol.)* **2014**, *3*, 44.
16. Dkhil, B.B.; Issa, A.; Denden, M. Germination and seedling emergence of primed okra (*Abelmoschus esculentus* L.) seeds under salt stress and low temperature. *Am. J. Plant Physiol.* **2014**, *9*, 38–45. [[CrossRef](#)]
17. Naz, F.; Gul, H.; Hamayun, M.; Sayyed, A.; Khan, H.; Sherwani, S. Effect of NaCl stress on *Pisum sativum* germination and seedling growth with the influence of seed priming with potassium (KCl and KOH). *Am.-Eurasian J. Agric. Environ. Sci.* **2014**, *14*, 1304–1311. [[CrossRef](#)]
18. Aloui, H.; Souguir, M.; Hannachi, C. Determination of an optimal priming duration and concentration protocol for pepper seeds (*Capsicum annuum* L.). *Acta Agric. Slov.* **2015**, *103*, 213–221. [[CrossRef](#)]
19. Zavariyan, A.M.; Rad, M.Y.; Asghari, M. Effect of seed priming by potassium nitrate on germination and biochemical indices in *Silybum marianum* L. under salinity stress. *Int. J. Life Sci.* **2015**, *9*, 23–29. [[CrossRef](#)]
20. Miladinov, Z.J.; Balešević-Tubić, S.N.; Đorđević, V.B.; Đukić, V.H.; Ilić, A.D.; Čobanović, L.M. Optimal time of soybean seed priming and primer effect under salt stress conditions. *J. Agric. Sci.* **2015**, *60*, 109–117. [[CrossRef](#)]
21. Stassinou, P.M.; Rossi, M.; Borromeo, I.; Capo, C.; Beninati, S.; Forni, C. Enhancement of *Brassica napus* Tolerance to High Saline Conditions by Seed Priming. *Plants* **2021**, *10*, 403. [[CrossRef](#)]
22. Paparella, S.; Araujo, S.S.; Rossi, G.; Wijayasinghe, M.; Carbonera, D.; Balestrazzi, A. Seed priming: State of the art and new perspectives. *Plant Cell Rep.* **2015**, *34*, 1281–1293. [[CrossRef](#)] [[PubMed](#)]
23. Lutts, S.; Paolo, B.; Lukasz, W.S.K.S.; Robert, P. Seed priming: New comprehensive approaches for an old empirical technique. In *New Challenges in Seed Biology-Basic and Translational Research Driving Seed Technology*; Intech Open: Rijeka, Croatia, 2016; pp. 1–4. [[CrossRef](#)]
24. Ibrahim, E.A. Seed priming to alleviate salinity stress in germinating seeds. *J. Plant Physiol.* **2016**, *192*, 38–46. [[CrossRef](#)] [[PubMed](#)]
25. Johnson, R.; Puthur, J.T. Seed priming as a cost effective technique for developing plants with cross tolerance to salinity stress. *Plant Physiol. Biochem.* **2021**, *162*, 247–257. [[CrossRef](#)] [[PubMed](#)]
26. Adnan, M.; Abd-ur-Rahman, H.; Asif, M.; Hussain, M.; Bilal, H.M.; Adnan, M.; Rehman, F.; Ahmad, S.; Khalid, M. Seed Priming; An Effective Way to Improve Plant Growth. *EC Agric.* **2020**, *6*, 01–05.
27. Farooq, M.; Irfan, M.; Aziz, T.; Ahmad, I.; Cheema, S.A. Seed priming with ascorbic acid improves drought resistance of wheat. *J. Agron. Crop Sci.* **2013**, *199*, 12–22. [[CrossRef](#)]
28. Iqbal, M.; Ashraf, M. Gibberellic acid mediated induction of salt tolerance in wheat plants: Growth, ionic partitioning, photosynthesis, yield and hormonal homeostasis. *Environ. Exp. Bot.* **2013**, *86*, 76–85. [[CrossRef](#)]
29. Ansari, O.; Azadi, M.S.; Sharif-Zadeh, F.; Younesi, E. Effect of hormone priming on germination characteristics and enzyme activity of mountain rye (*Secale montanum*) seeds under drought stress conditions. *J. Stress Physiol. Biochem.* **2013**, *9*, 61–71.
30. Chunthaburee, S.; Sanitchon, J.; Pattanagul, W.; Theerakulpisut, P. Alleviation of salt stress in seedlings of black glutinous rice by seed priming with spermidine and gibberellic acid. *Not. Bot. Horti Agrobot. Cluj-Napoca* **2014**, *42*, 405–413. [[CrossRef](#)]
31. Kubala, S.; Wojtyła, L.; Quinet, M.; Lechowska, K.; Lutts, S.; Garnczarska, M. Enhanced expression of the proline synthesis gene P5CSA in relation to seed osmopriming improvement of *Brassica napus* germination under salinity stress. *J. Plant Phys.* **2015**, *183*, 1–12. [[CrossRef](#)]
32. Dawood, M.G.; El-Awadi, M.E. Alleviation of salinity stress on *Vicia faba* L. plants via seed priming with melatonin. *Acta Biol. Colomb.* **2015**, *20*, 223–235. [[CrossRef](#)]
33. Mouradi, M.; Bouzigaren, A.; Farissi, M.; Latrach, L.; Qaddoury, A.; Ghoulam, C. Seed osmopriming improves plant growth, nodulation, chlorophyll fluorescence and nutrient uptake in alfalfa (*Medicago sativa* L.)–rhizobia symbiosis under drought stress. *Sci. Hortic.* **2016**, *213*, 232–242. [[CrossRef](#)]
34. Hasan, M.; Salam, M.; Chowdhury, M.; Sultana, M.; Islam, N. Effect of osmopriming on germination of rice seed. *Bang. J. Agril. Res.* **2016**, *41*, 451–460. [[CrossRef](#)]
35. Wang, Z.; Li, X.; Zhu, X.; Liu, S.; Song, F.; Liu, F.; Wang, Y.; Qi, X.; Wang, F.; Zuo, Z.; et al. Salt acclimation induced salt tolerance is enhanced by abscisic acid priming in wheat. *Plant Soil. Environ.* **2017**, *63*, 307–314. [[CrossRef](#)]
36. Ulfat, A.; Majid, S.A.; Hameed, A. Hormonal seed priming improves wheat (*Triticum aestivum* L.) field performance under drought and non-stress conditions. *Pak. J. Bot.* **2017**, *49*, 1239–1253.
37. Abid, M.; Hakeem, A.; Shao, Y.; Liu, Y.; Zahoor, R.; Fan, Y.; Suyu, J.; Tahir Ata-Ul-Karim, S.; Tian, Z.; Jiang, D.; et al. Seed osmopriming invokes stress memory against post-germinative drought stress in wheat (*Triticum aestivum* L.). *Environ. Exp. Bot.* **2018**, *145*, 12–20. [[CrossRef](#)]

38. Gharbi, E.; Lutts, S.; Dailly, H.; Quinet, M. Comparison between the impacts of two different modes of salicylic acid application on tomato (*Solanum lycopersicum*) responses to salinity. *Plant Signal. Behav.* **2018**, *13*, 5. [[CrossRef](#)] [[PubMed](#)]
39. Akter, L.; Fakir, O.A.; Alam, M.K.; Islam, M.U.; Chakraborti, P.; Alam, M.J.; Rashid, M.; Begum, M.; Kader, M. Amelioration of salinity stress in maize seed germination and seedling growth attributes through seed priming. *Open J. Soil. Sci.* **2018**, *8*, 137–146. [[CrossRef](#)]
40. Robledo, D.A.R. Effects of halopriming on seed germination and seedling emergence of *Capsicum frutescens*. *J. Bot. Res.* **2020**, *3*, 114–118. [[CrossRef](#)]
41. Sheteiwy, M.S.; Shao, H.; Qi, W.; Daly, P.; Sharma, A.; Shaghaleh, H.; Hamoud, Y.A.; El-Esawi, M.A.; Pan, R.; Wan, Q.; et al. Seed priming and foliar application with jasmonic acid enhance salinity stress tolerance of soybean (*Glycine max* L.) seedlings. *J. Sci. Food Agric.* **2021**, *101*, 2027–2041. [[CrossRef](#)]
42. El-Sanatawy, A.M.; Ash-Shormillesy, S.M.A.I.; Qabil, N.; Awad, M.F.; Mansour, E. Seed Halo-Priming Improves Seedling Vigor, Grain Yield, and Water Use Efficiency of Maize under Varying Irrigation Regimes. *Water* **2021**, *13*, 2115. [[CrossRef](#)]
43. Hidayah, A.; Nisak, R.R.; Susanto, F.A.; Nuringtyas, T.R.; Yamaguchi, N.; Purwestri, Y.A. Seed Halopriming Improves Salinity Tolerance of Some Rice Cultivars During Seedling Stage. *Bot. Stud.* **2022**, *63*, 24. [[CrossRef](#)]
44. Taghvaei, M.; Nasrolahizadehi, A.; Mastinu, A. Effect of Light, Temperature, Salinity, and Halopriming on Seed Germination and Seedling Growth of *Hibiscus sabdariffa* under Salinity Stress. *Agronomy* **2022**, *12*, 2491. [[CrossRef](#)]
45. Vidak, M.; Lazarević, B.; Nekić, M.; Šatović, Z.; Carović-Stanko, K. Effect of hormonal priming and osmopriming on germination of winter savory (*Satureja montana* L.) natural population under drought stress. *Agronomy* **2022**, *12*, 1288. [[CrossRef](#)]
46. Bisht, S.; Sharma, V.; Kumari, N. Biosynthesized magnetite nanoparticles from *Polyalthia longifolia* leaves improve photosynthetic performance and yield of *Trigonella foenum-graecum* under drought stress. *Plant Stress* **2022**, *5*, 100090. [[CrossRef](#)]
47. Cifuentes, L.; González, M.; Pinto-Irish, K.; Alvarez, R.; Coba de la Peña, T.; Ostria-Gallardo, E.; Franck, N.; Fischer, S.; Barros, G.; Castro, C.; et al. Metabolic imprint induced by seed halo-priming promotes a differential physiological performance in two contrasting quinoa ecotypes. *Front. Plant Sci.* **2023**, *13*, 1034788. [[CrossRef](#)]
48. Corbineau, F.; Picard, M.A.; Fougereux, J.A.; Ladonne, F.; Côme, D. Effects of dehydration conditions on desiccation tolerance of developing pea seeds as related to oligosaccharide content and cell membrane properties. *Seed Sci. Res.* **2000**, *10*, 329–339. [[CrossRef](#)]
49. Benamar, A.; Tallon, C.; Macherel, D. Membrane Integrity and Oxidative Properties of Mitochondria Isolated from Imbibing Pea Seeds after Priming or Accelerated Ageing. *Seed Sci. Res.* **2003**, *13*, 35–45. [[CrossRef](#)]
50. Pandita, V.K.; Anand, A.; Nagarajan, S. Enhancement of seed germination in hot pepper following pre-sowing treatments. *Seed Sci. Technol.* **2007**, *35*, 282–290. [[CrossRef](#)]
51. Sung, Y.; Cantliffe, D.J.; Nagata, R.T.; Nascimento, W.M. Structural Changes in Lettuce Seed During Germination at High Temperature Altered by Genotype, Seed Maturation Temperature, and Seed Priming. *J. Am. Soc. Hortic. Sci.* **2008**, *133*, 300–311. [[CrossRef](#)]
52. Chen, K.; Arora, R. Dynamics of the antioxidant system during seed osmopriming, post-priming germination, and seedling establishment in Spinach (*Spinacia oleracea*). *Plant Sci.* **2011**, *180*, 212–220. [[CrossRef](#)]
53. Chen, K.; Arora, R. Priming memory invokes seed stress-tolerance. *Environ. Exp. Bot.* **2013**, *94*, 33–45. [[CrossRef](#)]
54. Srivastava, A.K.; Suresh Kumar, J.; Suprasanna, P. Seed ‘primeomics’: Plants memorize their germination under stress. *Biol. Rev.* **2021**, *96*, 1723–1743. [[CrossRef](#)]
55. Ibrahim, E.A. Fundamental Processes Involved in Seed Priming. In *Priming and Pretreatment of Seeds and Seedlings*; Hasanuzzaman, M., Fotopoulos, V., Eds.; Springer: Singapore, 2019. [[CrossRef](#)]
56. Ali, S.; Charles, T.C.; Glick, B.R. Amelioration of high salinity stress damage by plant growth-promoting bacterial endophytes that contain ACC deaminase. *Plant Physiol. Biochem.* **2014**, *80*, 160–167. [[CrossRef](#)]
57. Kumar, A.; Singh, S.; Gaurav, A.K.; Srivastava, S.; Verma, J.P. Plant Growth-Promoting Bacteria: Biological Tools for the Mitigation of Salinity Stress in Plants. *Front. Microbiol.* **2020**, *11*, 1216. [[CrossRef](#)]
58. Rossi, M.; Borromeo, I.; Capo, C.; Glick, B.R.; Del Gallo, M.; Pietrini, F.; Forni, C. PGPB Improve Photosynthetic Activity and Tolerance to Oxidative Stress in *Brassica napus* Grown on Salinized Soils. *Appl. Sci.* **2021**, *11*, 11442. [[CrossRef](#)]
59. Stassinis, P.M.; Rossi, M.; Borromeo, I.; Capo, C.; Beninati, S.; Forni, C. Amelioration of salt stress tolerance in rapeseed (*Brassica napus*) cultivars by seed inoculation with *Arthrobacter globiformis*. *Plant. Biosyst.* **2022**, *156*, 370–383. [[CrossRef](#)]
60. Ramadoss, D.; Lakkineni, V.K.; Bose, P.; Ali, S.; Annapurna, K. Mitigation of salt stress in wheat seedlings by halotolerant bacteria isolated from saline habitats. *SpringerPlus* **2013**, *2*, 6. [[CrossRef](#)]
61. Brígido, C.; Nascimento, F.X.; Duan, J.; Glick, B.R.; Oliveira, S. Expression of an exogenous 1-aminocyclopropane-1-carboxylate deaminase gene in *Mesorhizobium* spp. reduces the negative effects of salt stress in chickpea. *FEMS Microbiol. Lett.* **2013**, *349*, 46–53. [[CrossRef](#)]
62. Tittabutr, P.; Piromyong, P.; Longtonglang, A.; Noisa-Ngiam, R.; Boonkerd, N.; Teaumroong, N. Alleviation of the effect of environmental stresses using co-inoculation of mung bean by *Bradyrhizobium* and rhizobacteria containing stress-induced ACC deaminase enzyme. *Soil. Sci. Plant. Nutr.* **2013**, *59*, 559–571. [[CrossRef](#)]
63. Ahmad, M.; Zahir, Z.A.; Nazli, F.; Akram, F.; Arshad, M.; Khalid, M. Effectiveness of halo-tolerant, auxin producing *Pseudomonas* and *Rhizobium* strains to improve osmotic stress tolerance in mung bean (*Vigna radiata* L.). *Braz. J. Microbiol.* **2013**, *44*, 1341–1348. [[CrossRef](#)]

64. Liu, Y.; Shi, Z.; Yao, L.; Yue, H.; Li, H.; Li, C. Effect of IAA produced by *Klebsiella oxytoca* Rs-5 on cotton growth under salt stress. *J. Gen. Appl. Microbiol.* **2013**, *59*, 59–65. [[CrossRef](#)]
65. Lim, J.H.; Kim, S.D. Induction of Drought Stress Resistance by Multi-Functional PGPR *Bacillus licheniformis* K11 in Pepper. *Plant. Pathol. J.* **2013**, *29*, 201–208. [[CrossRef](#)]
66. Bangash, N.; Khalid, A.; Mahmood, T.; Siddique, M.T. Screening rhizobacteria containing ACC-deaminase for growth promotion of wheat under water stress. *Pak. J. Bot.* **2013**, *45*, 91–96.
67. Aamir, M.; Aslam, A.; Khan, M.Y.; Usman, M. Co-inoculation with *Rhizobium* and plant growth promoting rhizobacteria (PGPR) for inducing salinity tolerance in mung bean under field condition of semi-arid climate. *Asian J. Agric. Biol.* **2013**, *1*, 7.
68. Jha, Y.; Subramanian, R.B. Paddy plants inoculated with PGPR show better growth physiology and nutrient content under saline condition. *Chil. J. Agric. Res.* **2013**, *73*, 213–219. [[CrossRef](#)]
69. Saghafi, K.; Ahmadi, J.; Asghar-zadeh, A.; Esmailizad, A. An Evaluation of the Influence of PGPR on Wheat Growth Indices under Saline Stress. *J. Sol. Biol.* **2013**, *1*, 47–59. [[CrossRef](#)]
70. Nautiyal, C.S.; Srivastava, S.; Chauhan, P.S.; Seem, K.; Mishra, A.; Sopory, S.K. Plant growth-promoting bacteria *Bacillus amyloliquefaciens* NBRISN13 modulates gene expression profile of leaf and rhizosphere community in rice during salt stress. *Plant. Physiol. Biochem.* **2013**, *66*, 1–9. [[CrossRef](#)]
71. Nakbanpote, W.; Panitlurtumpai, N.; Sangdee, A.; Sakulpone, N.; Sirisom, P.; Pimthong, A. Salt-tolerant and plant growth-promoting bacteria isolated from Zn/Cd contaminated soil: Identification and effect on rice under saline conditions. *J. Plant Interact.* **2014**, *9*, 379–387. [[CrossRef](#)]
72. Tewari, S.; Arora, N.K. Multifunctional exopolysaccharides from *Pseudomonas aeruginosa* PF23 involved in plant growth stimulation, biocontrol and stress amelioration in sunflower under saline conditions. *Curr. Microbiol.* **2014**, *69*, 484–494. [[CrossRef](#)]
73. Timmusk, S.; Abd El-Daim, I.A.; Copolovici, L.; Tanilas, T.; Kännaste, A.; Behers, L.; Nevo, E.; Seisenbaeva, G.; Stenström, E.; Niinemets, Ü. Drought-tolerance of wheat improved by rhizosphere bacteria from harsh environments: Enhanced biomass production and reduced emissions of stress volatiles. *PLoS ONE* **2014**, *9*, e96086. [[CrossRef](#)]
74. Zafar-ul-Hye, M.; Nasir, A.; Aon, M.; Hussain, S.; Ahmad, M.; Naz, I. Seed inoculation with *Pseudomonas fluorescens* and *Pseudomonas syringae* enhanced maize growth in a compacted saline-sodic soil. *Phyton* **2018**, *87*, 25–31.
75. Qin, S.; Zhang, Y.J.; Yuan, B.; Xu, P.Y.; Xing, J.; Wang, J.; Jiang, J.H. Isolation of ACC deaminase-producing habitat-adapted symbiotic bacteria associated with halophyte *Limonium sinense* (Girard) Kuntze and evaluating their plant growth-promoting activity under salt stress. *Plant Soil* **2014**, *374*, 753–766. [[CrossRef](#)]
76. Kim, K.; Jang, Y.J.; Lee, S.M.; Oh, B.T.; Chae, J.C.; Lee, K.J. Alleviation of salt stress by *Enterobacter* sp. EJ01 in tomato and *Arabidopsis* is accompanied by up-regulation of conserved salinity responsive factors in plants. *Mol. Cells* **2014**, *37*, 109–117. [[CrossRef](#)]
77. Yan, J.M.; Smith, M.D.; Glick, B.R.; Liang, Y. Effects of ACC deaminase containing rhizobacteria on plant growth and expression of Toc GPases in tomato (*Solanum lycopersicum*) under salt stress. *Botany* **2014**, *92*, 775–781. [[CrossRef](#)]
78. Egamberdieva, D.; Jabborova, D.; Hashem, A. *Pseudomonas* induces salinity tolerance in cotton (*Gossypium hirsutum*) and resistance to *Fusarium* root rot through the modulation of indole-3-acetic acid. *Saudi J. Biol. Sci.* **2015**, *22*, 773–779. [[CrossRef](#)]
79. Sukweenadhi, J.; Kim, Y.J.; Choi, E.S.; Koh, S.C.; Lee, S.W.; Kim, Y.J.; Yang, D.C. *Paenibacillus yonginensis* DCY84T induces changes in *Arabidopsis thaliana* gene expression against aluminum, drought, and salt stress. *Microbiol. Res.* **2015**, *172*, 7–15. [[CrossRef](#)]
80. Bhatt, S.; Pandhi, N.; Raghav, R. Improved salt tolerance and growth parameters of groundnut (*Arachis hypogaea* L.) employing Halotolerant *Bacillus cereus* SVSCD1 isolated from Saurashtra Region, Gujarat. *Ecol. Environ. Conserv.* **2020**, *26*, S199–S212.
81. Ni, H.; Wu, Y.; Zong, R.; Ren, S.; Pan, D.; Yu, L.; Li, J.; Qu, Z.; Wang, Q.; Zhao, G.; et al. Combination of *Aspergillus niger* MJ1 with *Pseudomonas stutzeri* DSM4166 or mutant *Pseudomonas fluorescens* CHA0-*nif* improved crop quality, soil properties, and microbial communities in barrier soil. *Front. Microbiol.* **2023**, *14*, 1064358. [[CrossRef](#)]
82. Han, Y.; Wang, R.; Yang, Z.; Zhan, Y.; Ma, Y.; Ping, S.; Zhang, L.; Lin, M.; Yan, Y. 1-Aminocyclopropane-1-Carboxylate Deaminase from *Pseudomonas stutzeri* A1501 Facilitates the Growth of Rice in the Presence of Salt or Heavy Metals. *J. Microbiol. Biotechnol.* **2015**, *25*, 1119–1128. [[CrossRef](#)]
83. Saleem, A.R.; Bangash, N.; Mahmood, T.; Khalid, A.; Centritto, M.; Siddique, M.T. Rhizobacteria capable of producing ACC deaminase promote growth of velvet bean (*Mucuna pruriens*) under water stress condition. *Int. J. Agric. Biol.* **2015**, *17*, 663–667. [[CrossRef](#)]
84. Kiani, M.Z.; Ali, A.; Sultan, T.; Ahmad, R.; Hydar, S.I. Plant growth promoting rhizobacteria having 1-aminocyclopropane-1-carboxylic acid deaminase to induce salt tolerance in sunflower (*Helianthus annuus* L.). *Nat. Res.* **2015**, *6*, 391–397. [[CrossRef](#)]
85. Siddikee, M.A.; Sundaram, S.; Chandrasekaran, M.; Kim, K.; Selvakumar, G.; Sa, T. Halotolerant bacteria with ACC deaminase activity alleviate salt stress effect in canola seed germination. *J. Korean Soc. Appl. Biol. Chem.* **2015**, *58*, 237–241. [[CrossRef](#)]
86. Lee, G.W.; Lee, K.J.; Chae, J.C. *Herbaspirillum* sp. strain GW103 alleviates salt stress in *Brassica rapa* L. ssp. *pekinensis*. *Protoplasma* **2016**, *253*, 655–661. [[CrossRef](#)]
87. Kumar, M.; Mishra, S.; Dixit, V.; Kumar, M.; Agarwal, L.; Chauhan, P.S.; Nautiyal, C.S. Synergistic effect of *Pseudomonas putida* and *Bacillus amyloliquefaciens* ameliorates drought stress in chickpea (*Cicer arietinum* L.). *Plant Signal. Behav.* **2016**, *11*, e1071004. [[CrossRef](#)]
88. Chauhan, P.S.; Lata, C.; Tiwari, S.; Chauhan, A.S.; Mishra, S.K.; Agrawal, L.; Chakrabarty, D.; Nautiyal, C.S. Transcriptional alterations reveal *Bacillus amyloliquefaciens*-rice cooperation under salt stress. *Sci. Rep.* **2019**, *9*, 11912. [[CrossRef](#)]

89. Vimal, S.R.; Patel, V.K.; Singh, J.S. Plant growth promoting *Curtobacterium albidum* strain SRV4: An agriculturally important microbe to alleviate salinity stress in paddy plants. *Ecol. Indic.* **2019**, *105*, 553–562. [[CrossRef](#)]
90. Kim, J.E.; Woo, O.G.; Bae, Y.; Keum, H.L.; Chung, S.; Sul, W.J.; Lee, J.H. Enhanced drought and salt stress tolerance in *Arabidopsis* by *Flavobacterium crocinum* HYN0056^T. *Plant Biol.* **2020**, *63*, 63–71. [[CrossRef](#)]
91. Lee, D.G.; Lee, J.M.; Choi, C.G.; Lee, H.; Moon, J.C.; Chung, N. Effect of plant growth-promoting rhizobacterial treatment on growth and physiological characteristics of *Triticum aestivum* L. under salt stress. *Appl. Biol. Chem.* **2021**, *64*, 89. [[CrossRef](#)]
92. Shaffique, S.; Khan, M.A.; Wani, S.H.; Imran, M.; Kang, S.-M.; Pande, A.; Adhikari, A.; Kwon, E.-H.; Lee, I.-J. Biopriming of Maize Seeds with a Novel Bacterial Strain SH-6 to Enhance Drought Tolerance in South Korea. *Plants* **2022**, *11*, 1674. [[CrossRef](#)]
93. Beckers, G.J.M.; Conrath, U. Priming for stress resistance: From the lab to the field. *Curr. Opin. Plant Biol.* **2007**, *10*, 425–431. [[CrossRef](#)]
94. Gamalero, E.; Glick, B.R. Recent Advances in Bacterial Amelioration of Plant Drought and Salt Stress. *Biology* **2022**, *11*, 437. [[CrossRef](#)] [[PubMed](#)]
95. Oyedoh, O.P.; Yang, W.; Dhanasekaran, D.; Santoyo, G.; Glick, B.R.; Babalola, O.O. Sustainable Agriculture: Rare-Actinomycetes to the Rescue. *Agronomy* **2023**, *13*, 666. [[CrossRef](#)]
96. Glick, B.R.; Penrose, D.M.; Li, J. A model for the lowering of plant ethylene concentrations by plant growth promoting bacteria. *J. Theor. Biol.* **1998**, *190*, 63–68. [[CrossRef](#)] [[PubMed](#)]
97. Pellegrini, M.; Pagnani, G.; Rossi, M.; D'Egidio, S.; Del Gallo, M.; Forni, C. *Daucus carota* L. seed inoculation with a consortium of bacteria improves plant growth and soil fertility status and microbial community. *Appl. Sci.* **2021**, *11*, 3274. [[CrossRef](#)]
98. Djebaili, R.; Pellegrini, M.; Rossi, M.; Forni, C.; Smati, M.; Del Gallo, M.; Kitouni, M. Characterization of Plant Growth-Promoting traits and inoculation effects on *Triticum durum* of Actinomycetes isolates under salt stress conditions. *Soil. Syst.* **2021**, *5*, 26. [[CrossRef](#)]
99. Raza, A.; Charagh, S.; Salehi, H.; Abbas, S.; Saeed, F.; Poinern, G.E.J.; Siddique, K.H.M.; Varshney, R.K. Nano-enabled stress-smartagriculture: Can nanotechnology deliver drought and salinity-smart crops? *J. Sustain. Agric. Environ.* **2023**, *2*, 189–214. [[CrossRef](#)]
100. Acharya, P.; Jayaprakasha, G.K.; Crosby, K.M.; Jifon, J.L.; Patil, B.S. Green-Synthesized Nanoparticles Enhanced Seedling Growth, Yield, and Quality of Onion (*Allium cepa* L.). *ACS Sustain. Chem. Eng.* **2019**, *7*, 14580–14590. [[CrossRef](#)]
101. Do Espirito Santo Pereira, A.; Caixeta Oliveira, H.; Fernandes Fraceto, L.; Santaella, C. Nanotechnology Potential in Seed Priming for Sustainable Agriculture. *Nanomaterials* **2021**, *11*, 267. [[CrossRef](#)]
102. Pérez-de-Luque, A. Interaction of Nanomaterials with Plants: What Do We Need for Real Applications in Agriculture? *Front. Environ. Sci.* **2017**, *5*, 12. [[CrossRef](#)]
103. Kandhol, N.; Jain, M.; Tripathi, D.K. Nanoparticles as potential hallmarks of drought stress tolerance in plants. *Physiol. Plant* **2022**, *174*, e13665. [[CrossRef](#)]
104. Avramova, Z. Transcriptional ‘memory’ of a stress: Transient chromatin and memory (epigenetic) marks at stress-response genes. *Plant J.* **2015**, *83*, 149–159. [[CrossRef](#)]
105. Sadhukhan, A.; Prasad, S.S.; Mitra, J.; Siddiqui, N.; Sahoo, L.; Kobayashi, Y.; Koyama, H. How do plants remember drought? *Planta* **2022**, *256*, 7. [[CrossRef](#)]
106. Ding, Y.; Fromm, M.; Avramova, Z. Multiple exposures to drought ‘train’ transcriptional responses in *Arabidopsis*. *Nat. Commun.* **2012**, *3*, 740. [[CrossRef](#)]
107. Ding, Y.; Liu, N.; Virilouvet, L.; Riethoven, J.J.; Fromm, M.; Avramova, Z. Four distinct types of dehydration stress memory genes in *Arabidopsis thaliana*. *BMC Plant Biol.* **2013**, *13*, 229. [[CrossRef](#)] [[PubMed](#)]
108. Virilouvet, L.; Fromm, M. Physiological and transcriptional memory in guard cells during repetitive dehydration stress. *New Phytol.* **2015**, *205*, 596–607. [[CrossRef](#)] [[PubMed](#)]
109. Van Hulten, M.; Pelser, M.; Van Loon, L.C.; Pieterse, C.M.; Ton, J. Costs and benefits of priming for defense in *Arabidopsis*. *Proc. Natl. Acad. Sci. USA* **2006**, *103*, 5602–5607. [[CrossRef](#)] [[PubMed](#)]
110. Galviz, Y.C.F.; Ribeiro, R.V.; Souza, G.M. Yes, plants do have memory. *Theor. Exp. Plant Physiol.* **2020**, *32*, 195–202. [[CrossRef](#)]
111. Soja, G.; Eid, M.; Gangl, H.; Redl, H. Ozone sensitivity of grapevine (*Vitis vinifera* L.): Evidence for a memory effect in a perennial crop plant? *Phyton. Ann. Rev. Bot.* **1997**, *37*, 265–270.
112. Skirycz, A.; Inzé, D. More from less: Plant growth under limited water. *Curr. Opin. Biotechnol.* **2010**, *21*, 197–203. [[CrossRef](#)]
113. Santangeli, M.; Capo, C.; Beninati, S.; Pietrini, F.; Forni, C. Gradual Exposure to Salinity Improves Tolerance to Salt Stress in Rapeseed (*Brassica napus* L.). *Water* **2019**, *11*, 1667. [[CrossRef](#)]
114. Crisp, P.A.; Ganguly, D.; Eichten, S.R.; Borevitz, J.O.; Pogson, B.J. Reconsidering plant memory: Intersections between stress recovery, RNA turnover, and epigenetics. *Sci. Adv.* **2016**, *2*, e1501340. [[CrossRef](#)] [[PubMed](#)]
115. Gagliano, M.; Renton, M.; Depczynski, M.; Mancuso, S. Experience teaches plants to learn faster and forget slower in environments where it matters. *Oecologia* **2014**, *175*, 63–72. [[CrossRef](#)] [[PubMed](#)]
116. Conrath, U.; Beckers, G.J.; Flors, V.; García-Agustín, P.; Jakab, G.; Mauch, F.; Newman, M.A.; Pieterse, C.M.J.; Poinssot, B.; Pozo, M.J.; et al. Priming: Getting ready for battle. *Mol. Plant-Microbe Interact.* **2006**, *19*, 1062–1071. [[CrossRef](#)] [[PubMed](#)]
117. Hossain, M.A.; Burritt, D.J.; Fujita, M. Cross-stress tolerance in plants: Molecular mechanisms and possible involvement of reactive oxygen species and methylglyoxal detoxification systems. In *Abiotic Stress Response in Plants*; Tuteja, N., Gill, S.S., Eds.; Wiley: New York, NY, USA, 2016; pp. 323–375. [[CrossRef](#)]

118. Galis, I.; Gaquerel, E.; Pandey, S.P.; Baldwin, I.T. Molecular mechanisms underlying plant memory in JA-mediated defence responses. *Plant Cell Environ.* **2009**, *32*, 617–627. [[CrossRef](#)] [[PubMed](#)]
119. Li, Z.G.; Gong, M. Mechanical stimulation-induced cross-adaptation in plants: An overview. *J. Plant Biol.* **2011**, *54*, 358–364. [[CrossRef](#)]
120. Li, X.; Cai, J.; Liu, F.; Dai, T.; Cao, W.; Jiang, D. Physiological, proteomic and transcriptional responses of wheat to combination of drought or waterlogging with late spring low temperature. *Funct. Plant Biol.* **2014**, *41*, 690–703. [[CrossRef](#)]
121. Faralli, M.; Lektemur, C.; Rosellini, D.; Gürel, F. Effects of heat shock and salinity on barley growth and stress-related gene transcription. *Biol. Plant* **2015**, *59*, 537–546. [[CrossRef](#)]
122. Zhang, X.; Wang, X.; Zhong, J.; Zhou, Q.; Wang, X.; Cai, J.; Dai, T.; Cao, W.; Jiang, D. Drought priming induces thermo-tolerance to post-anthesis high-temperature in offspring of winter wheat. *Environ. Exp. Bot.* **2016**, *127*, 26–36. [[CrossRef](#)]
123. Liu, X.; Quan, W.; Bartels, D. Stress memory responses and seed priming correlate with drought tolerance in plants: An overview. *Planta* **2022**, *255*, 45. [[CrossRef](#)]
124. Gerke, J. Phytate (Inositol hexakisphosphate) in soil and phosphate acquisition from inositol phosphates by higher plants. A Review. *Plants* **2015**, *4*, 253–266. [[CrossRef](#)]
125. Godoy, F.; Olivos-Hernández, K.; Stange, C.; Handford, M. Abiotic Stress in Crop Species: Improving Tolerance by Applying Plant Metabolites. *Plants* **2021**, *10*, 186. [[CrossRef](#)] [[PubMed](#)]
126. Zulfiqar, F.; Nafees, M.; Chen, J.; Darras, A.; Ferrante, A.; Hancock, J.T.; Ashraf, M.; Zaid, A.; Latif, N.; Corpas, F.J.; et al. Chemical priming enhances plant tolerance to salt stress. *Front. Plant Sci.* **2022**, *13*, 946922. [[CrossRef](#)] [[PubMed](#)]
127. Pagano, A.; Macovei, A.; Balestrazzi, A. Molecular dynamics of seed priming at the crossroads between basic and applied research. *Plant Cell Rep.* **2023**, *42*, 657–688. [[CrossRef](#)] [[PubMed](#)]

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