frontiers | Frontiers in Environmental Science

TYPE Review
PUBLISHED 05 October 2022
DOI 10.3389/fenvs.2022.991977

OPEN ACCESS

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SPECIALTY SECTION
This article was submitted to Environmental Economics and Management, a section of the journal Frontiers in Environmental Science

RECEIVED 12 July 2022
ACCEPTED 16 August 2022
PUBLISHED 05 October 2022

CITATION
Khan MO, Irfan M, Muhammad A, Ullah I, Nawaz S, Khalil MK and Ahmad M (2022), A practical and economical strategy to mitigate salinity stress through seed priming.
Front. Environ. Sci. 10:991977.
doi: 10.3389/fenvs.2022.991977

A practical and economical strategy to mitigate salinity stress through seed priming

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Soil salinity is one of the significant abiotic threats to crops that deteriorates crop yields, and the world's increasing population faces serious food problems due to abiotic threats. It is one of the major abiotic problems affecting more than 30% of irrigated land across the globe. The concentrations of various salts, such as NaCl, KCl, Na_2SO_4, and Na_2CO_3, cause saline stress; however, NaCl is the most abundant salt in the soil. Salinity could affect seed germination due to osmotic potential or due to specific toxic ion effects, and it decreases germination percentage and increases germination time, and high salt stress is responsible for delaying seed germination. Therefore, it is necessary to alleviate the negative impact of soil salinity during seedling growth periods, so the growth of crops in salt-affected soil will be much more enhanced. Seed priming is the utmost effective technique that could mitigate the harmful impact of soil salinity. This methodology not only minimizes the salinity tolerance but also strengthens the defense system of crops. In this technique, the hydration level within the seeds is controlled by applying pre-sowing treatments, allowing specific pre-germinative metabolic processes to occur and preventing radical emergence. Seed priming also decreases the seed germination time and improves antioxidant enzyme activities, stopping or minimizing reactive oxygen species' adverse effects. It enhances the seedling performance with rapid and homogenous germination and vigorous and dynamic growth of the seedling, achieving a physiological situation leading to quick and enhanced emergence and germination of various crops. This review covers the mechanisms of seed priming, salinity tolerance, seed priming crosstalk with salinity tolerance, and seed priming techniques that induce biochemical, physiological, and morphological mechanisms in saline stress. Further research needs to be performed on advanced seed priming methods such as priming with nanoparticles and seed priming with physical agents (UV

Abbreviations: AA, ascorbic acid; APX, ascorbate peroxidase; DHNs, dehydrins; GR, glutathione reductase; ABA, abscisic acid; CAT, catalase; HSPs, heat shock proteins; LEA, late embryogenic abundance; MDA, malondialdehyde; POD, peroxidase; POX, peroxidase reductase; ROS, reactive oxygen species; SOD, superoxide dismutase.

radiation, X-rays, gamma rays, and microwaves) to minimize the negative impact of salinity stress on different crops under different harsh environmental conditions.

KEYWORDS

soil salinity, seed priming, abiotic stress, antioxidant enzymes, ROS

Introduction

Extreme temperature, drought, heavy metal toxicity, and soil salinity are the primary damaging abiotic plant stresses. A harsh environmental condition applies a considerable amount of stress on plants' existence in which salinity is the principal prevailing abiotic stress. This sharply hinders the growth of the plant and developmental processes and brings a substantial annual loss in the yield (Mbarki et al., 2018; Safdar et al., 2019). The impact of salinity stress is more dominant in coastal, arid, and semi-arid areas of the world (Shalaby and El-Messairy, 2018). Saline soils contain various dissolved salts, including NaCl, $MgSO_4$, Na_2SO_4, KCl, $MgCl_2$, $CaSO_4$, and Na_2CO_3. These salts' presence contributes to salt stress; however, NaCl, among other salts, is the most predominant salt and focuses on salinity studies. Accumulation of higher salts occurs in the upper top 10 cm layer of the soil than in lower soil layers (Esechie, 1995; Al-Saady et al., 2012). Seeds of cultivated plants are generally sown in the top layer of the soil. Salinity is becoming more widespread due to less sustainable irrigation practices, less effective salinity reclamation methods, and bringing marginal area for crop production (Kang et al., 2014; Kopittke et al., 2019). The saline soils exceed 800 million hectares worldwide, which is nearly about 6 percent of the world's entire land area (Munns and Tester 2008; FAO, 2011). According to the FAO (2011), water-logging and interrelated salinity have adversely influenced 60–80 million hectares of soil. Soil deteriorated by salinity is not less than 10 mha of agricultural soil annually worldwide, and land degradation due to salinity is a very significant problem worldwide, which has negatively affected land productivity (Qadir et al., 2014; Hossain et al., 2020). At the end of the 21st century, more than 50% of agricultural land will be lost due to soil salinity problems (FAO, 2011).

Soil salinity influences plants' growth at all developmental periods, but it varies from one growth stage to another. Seed germination is a critical growth stage that could be negatively affected by high salinity. The survival of plants during germination and emergence is considered the most important sign of tolerance to salt. Therefore, most crop species are salt sensitive at the early stages of growth, comprising seedling and germination growth stages (Wang and Han, 2009). Restricted water uptake results from biochemical, physiological, and structural changes in a germinating seed and is the ultimate reason for poor seed germination (M. A. Ashraf and Ashraf, 2012; M. Ashraf and Foolad, 2005). Adaptation of plants to a saline environment during growth stages (germination and early seedling growth) is critical for stand establishment. The germination initiation was delayed in susceptible plant seeds due to salinity stress (E. A. Ibrahim, 2016). Soil salinity stress is also responsible for seedling establishment and slow germination of seeds (Q. Ali et al., 2017; Jisha et al., 2013). Additionally, in later stages after stand establishment, the Na^+ toxic concentration in leaves encourages a decline in photosynthesis and premature leaf senescence by limiting carbon assimilation (Hussain S. et al., 2018; Saddiq et al., 2019). A high salt concentration reduces percentage germination and extends germination time (Sucre and Suárez, 2011; Ansari et al., 2019). The amount and percentage of germination of germinating seeds fluctuate at a specific time among cultivars and species. Läuchli and Grattan, 2007 reported a comprehensive relationship between time and percentage of germination after water addition at various salt levels. Salinity could affect plant growth and seed germination by creating osmotic stress or specific ion effects. This results in stomatal closure and imbibition of several biochemical and physiological paths, which include uptake of nutrients (like K^+ and Ca^{+2}) and CO_2 assimilation (Safdar et al., 2019; H. Alam et al., 2021b; Fu et al., 2020; Parihar et al., 2015). Soil salinity stress causes a reduction in the early growth rate of crops. The reductions in plant growth due to greater salinity result from

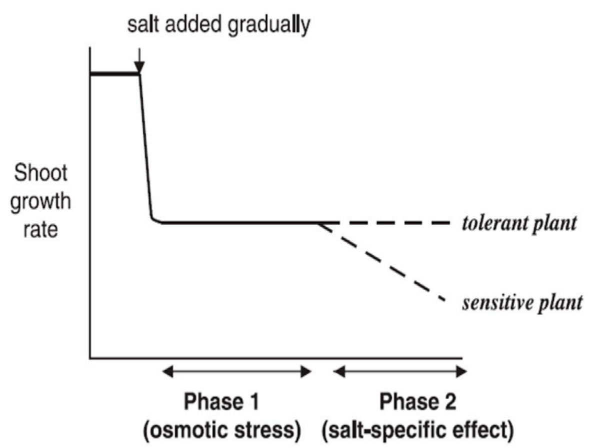

FIGURE 1
Salinity induces a two-phase growth performance in different salt-sensitive plants (Munns, 2005).

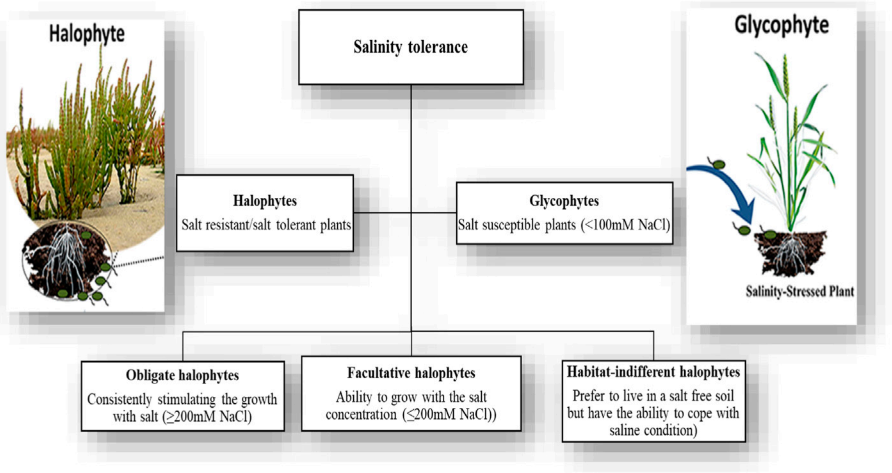

FIGURE 2
Classification of plants based on salinity stress tolerance.

specific ion effect (high Na^+ and Cl^- ions) and osmotic effect, which induce a water deficit situation on critical biochemical processes (Munns and Tester, 2008; Hasanuzzaman et al., 2013; Marriboina et al., 2017). The inhibition of plant growth due to salinity stress in soil water is because of two reasons. First, it creates an osmotic effect, and second, it causes a salt-specific ion effect. These two effects of saline stress give rise to a two-stage growth response to salt (Munns, 1993, 2005) (Figure 1).

Salinity tolerance

Salinity tolerance can be defined as crops' ability to grow well and complete their life cycle in high saline soil. Crops are generally classified into two groups (halophytes and glycophytes) based on their tolerance to salts. Halophytes are those plants that can grow well in a saline environment and tolerate a high level of salt stress, while glycophytes are highly salt-sensitive plants that cannot tolerate a high concentration of salt stress (Ellouzi et al., 2011; Hapani and Marjadi, 2015) (Figure 2). There is a great difference between species and even cultivars based on their ability to tolerate salinity stress (Izadi et al., 2014).

Seed priming crosstalk with salinity tolerance

Rapid germination of seeds and stand establishment are essential aspects that influence crop production in stressful environments. Therefore, it is vital to improve cultivated crop tolerance to high salinity stress. Different strategies are used to improve the salinity tolerance of other cultivated crops; one of the best approaches is seed priming, which has been evaluated as an active method to alleviate salinity stress (Munns and Gilliham, 2015; Banerjee and Roychoudhury, 2018; Farooq et al., 2019). This methodology minimizes the abiotic stress tolerance; moreover, it strengthens the protection system of crops. In this technique, the hydration level within the seeds is controlled by applying pre-sowing treatments, allowing specific pre-germinative metabolic processes to occur and preventing radical emergence (M. A. Ashraf and Ashraf, 2012; M. Ashraf and Foolad, 2005; Lutts et al., 2016; D. Singh and Kumar, 2021). Such a phenomenon is termed as enhanced stimulation defense mechanisms of a plant (Anderson et al., 2017; Yang et al., 2022). Seed priming decreases the time duration between planting and the emergence of a seed. It induces physiological modification within the target seeds, which consume natural and synthetic compounds within their pre-germination period. It is a beneficial technique for modifying seed quality through specific germinative metabolic processes, which involve osmotic adjustments, membrane reorganization and restructure, and retarding of electrolyte seepage (Mansour et al., 2019; Srivastava et al., 2021). It also helps in DNA replication responses, antioxidant function, more ATP availability, and encouraged protein biosynthesis, restoring cellular bio-membranes, and improving antioxidant enzymes (Chen and Arora, 2013; Hussain et al., 2015; Hussain et al., 2019; Mansour et al., 2019; Sen and Puthur, 2020). Anaytullah 2007 stated that the seed priming process strengthens the biochemical status of plants by inducing the activity of hydrolyses (e.g., amylase) and levels of sugars in germination whereas the enzyme (nitrate reductase) and nitrogen content in seedlings under normal conditions concerning unprimed seeds. Moreover, the seed priming role has been well

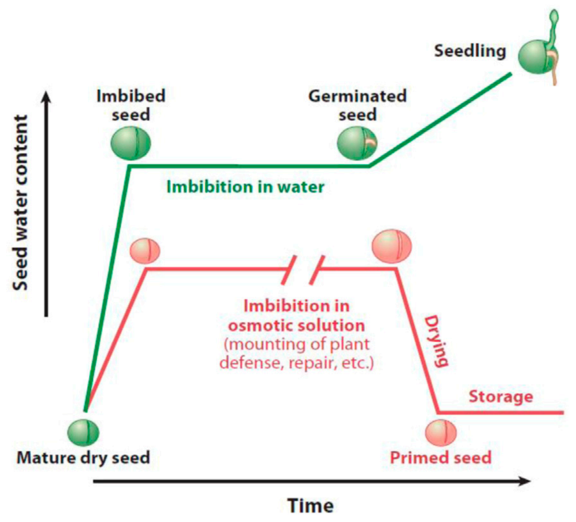

FIGURE 3
Graphical demonstration of the water uptake inside the seed in the seed priming process and standard germination (Rajjou et al., 2012).

known in improving germination and growth of various crops under various abiotic stresses (Hussain M. I. et al., 2018; Jisha et al., 2013). The antioxidant enzyme defense system enhanced in primed seeds, which has improved levels of superoxide dismutase (SOD), catalase (CAT), glutathione reductase (GR), peroxidase (POD), and ascorbic acid and regulates stress proteins, i.e., aquaporin, dehydrins (DHNs), and late embryogenesis abundant proteins (Blokhina et al., 2003; Chen and Arora, 2013; Zhu et al., 2017). Seed priming enhances the performance of seeds with rapid and homogenous germination and vigorous growth of seedlings, producing favorable physiological conditions which lead to faster and healthier germination of various crops (Abdel-Moneim Khafagy, 2017; A. Khan et al., 2017; Mondo et al., 2016; Patel et al., 2017; Yücel and Heybet, 2016).

Mechanism of seed priming

A method before sowing involves partly hydration of seeds for a specific period in a particular environment followed by drying; this phenomenon is usually termed as seed priming. Seed priming is an essential and effective strategy that provides a vital defense mechanism and abiotic stress tolerance. Seed priming allows the physiochemical processes (metabolic activities) before germination in treated seeds, keeping the optimum hydration level before sowing and restricting radicle emergence (Ahmad et al., 2021; do Espirito Santo Pereira et al., 2021; Hussain et al., 2019; E. A. Ibrahim, 2016; Hussain et al., 2015; Lutts et al., 2016; Sheteiwy et al., 2021). The priming process permits processes required for germination before germination. Seed priming in water contributes to metabolic changes essential for germination like breaking seed dormancy, activation of enzymes, and water imbibition (Ajouri et al., 2004; Dagar et al., 2021; Islam et al., 2021; Rehman et al., 2021; Bhardwaj et al., 2022). Germination requires moisture; therefore, seed priming provides moisture suitable for germination, which is just less than the actual moisture necessary for germination, however, ideal for metabolic processes involved in germination (Khan M. I. et al., 2021; Cao et al., 2022; Dagar et al., 2022; Khan et al., 2022).

Additionally, seed hydration activates germination in three phases: lag phase, imbibition, and radicle protrusion over the testa (E. A. Ibrahim, 2016). The water supply is controlled to seed in seed priming to make the seed moisture at a level needed for actual germination. This level is sufficient to initiate various physiological processes linked with the early phase of germination; however, the seed transition is avoided toward complete germination (M. Ashraf and Foolad, 2005; Jisha et al., 2013; Nawaz et al., 2013; Paparella et al., 2015). The initial growth stages, in which phase III is avoided, whereas the lag and hydration phases, also known as phase II and phase I, are achieved by primed seeds (Moreno et al., 2018; E. A.-A. Ibrahim, 2019). Before completing germination, the reserves (nutrients and moisture) in primed seeds are actually converted that efficiently nourish the newly formed embryo. When suitable environmental conditions are achieved, the primed seeds transfer to the next (third) phase of germination, i.e., protrusion of the radicle (Rajjou et al., 2012; E. A. Ibrahim, 2016; Kubala et al., 2015a) (Figure 3).

Before seeds dry, the treated seeds are rinsed and dried to the optimum level essential for seed storage. Seeds are dried after priming to attain a vital benefit of storing seeds and having a beneficial effect of maintaining quality and avoiding the worsening of seeds (Di Girolamo and Barbanti, 2012; Bhanuprakash, 2015; Pawar and Laware, 2018; Sano et al., 2020). Seed vigor and viability are affected by seed drying once the radicle emergence initiates; however, this can be managed in phase III without any loss by gaining starter moisture (E. A. Ibrahim, 2016; Rajjou et al., 2012). The treated or primed seed possesses two vital qualities of dryness (desiccation tolerance) and durability (longevity), for which these treated seeds can be stored up to sowing (M. A. Ashraf and Ashraf, 2012; M. Ashraf and Foolad, 2005). Durability or longevity is very closely associated with storage and dehydration procedures. Rapid dehydration might vary the soluble carbohydrate content, and the desiccation tolerance and slow dehydration of these treated seeds increase the seed's durability (Khalaki et al., 2021). Primed seeds are useful to be stored, but their life span compared to non-primed seeds is less; therefore, an optimal storage condition is highly recommended to avoid any seed damage during the storage period.

Priming is not a simple emulation of the early imbibition germination phase. It is responsible for activating the stress-

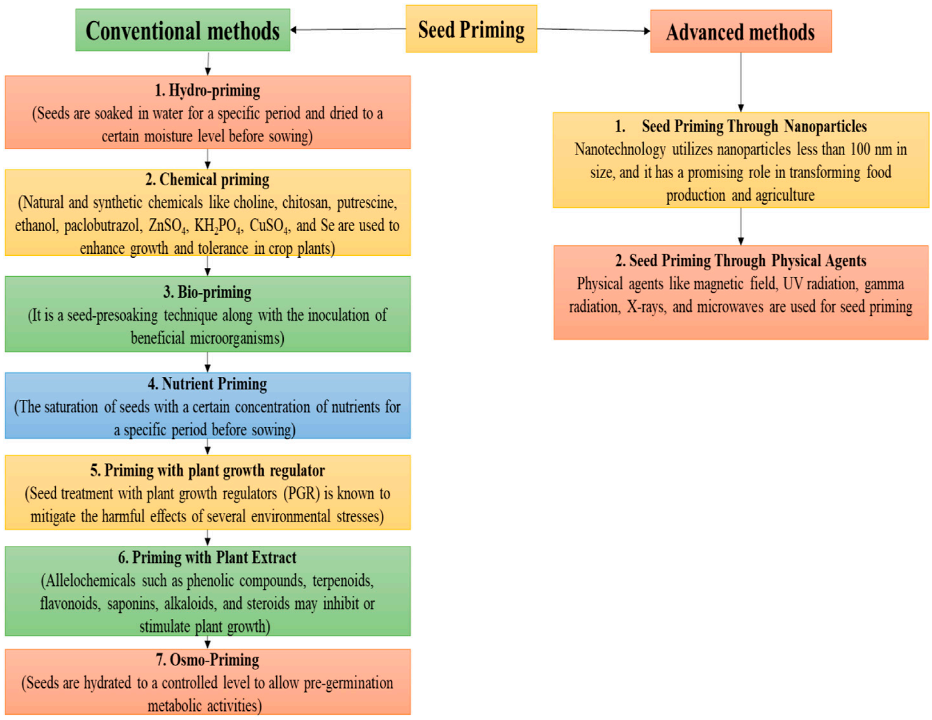

FIGURE 4
Schematic diagram of different seed priming methods.

responsive system by imposing adequate stress on seeds, which confers a cross-tolerance on seeds when it opens to future stresses (Bhanuprakash and Yogeesha, 2016). In the early germination phase, metabolic activities took place in primed seeds such as RNA and protein production, structural (membrane fortification in imbibition time), and genetic repair and antioxidant mechanisms. These processes are responsible for seedling growth and good germination (Saddiq et al., 2019; Li et al., 2021, 2022).

Seed priming techniques

Seed priming could be conducted by using conventional and advanced methods as shown in Figure 4. Conventional methods include halo-priming (seeds soaked in salt solutions), hydro-priming, osmopriming, solid matrix priming, and bio-stimulators (ASA and SA) (Abdel-Moneim Khafagy, 2017; A. Khan et al., 2017; A. Z. Khan and Muhammad, 2017; Mondo et al., 2016; Ruttanaruangboworn et al., 2017). Advanced methods include seed priming with nanoparticles and seed priming through physical agents (UV radiation, X-rays, and microwaves). Halo-priming includes soaking of seeds in brine solutions (KCl and NaCl) up to concentrations of 50–200 mM (Afzal et al., 2008; Shabala and Munns, 2012; El-Sanatawy et al., 2021; M. Kumar et al., 2016; Sahab et al., 2020). Again, seed treatment's critical role before sowing with different salt concentrations is to encourage salt tolerance against salinity in emerging seedlings (Basra et al., 2005). The published literature review has indicated that halo-priming with $CaCl_2$ and KCl mitigates salinity stress by regulating seedling growth, phenolic and proline concentration, and photosynthetic activity (A. Khan et al., 2019a, Khan A. et al., 2021; M. Kumar et al., 2016).

Table 1 presents that seed priming with $CaCl_2$ has increased shoot fresh and dry weight, root fresh and dry weight, and root length, except for root and shoot Na^+ concentration in wheat varieties (Khan M. N. et al., 2019). Different priming techniques improved the height of the plant, chlorophylls a and b, leaf area, total soluble protein and phenolics, glycine betaine, proline, K^+ content, osmotic potential, cell membrane stability, relative water content, grain yield, and harvest index while decreasing leaf MDA and Na^+ content under each level of imposed salinity in barley (Tabassum et al., 2018). Mehboob et al. (2018) concluded that different priming techniques followed by redrying and surface drying were the most effective in enhancing seedling emergence and maize crop growth. Soil salinity deleteriously affected seed germination, seedling potency, plant establishment, and yield of crops. Ali et al. (2017)

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TABLE 1 Effect of various priming agents to alleviate salinity stress in different crops.

Crop	Agent of priming	Critical results of seed priming	Reference
Triticum aestivum	KCl and NaCl (50 mM)	Increased final emergence percentage and emergence index and decreased emergence time	Saddiq et al. (2019)
Triticum aestivum	$CaCl_2$ (50 mM)	Enhanced weight of fresh and dry shoot and root and root length and reduced Na+ content in the shoot and root	M. N. Khan et al. 2019b
Zea mays L., *Pisum sativum* Var. *Lathyrus sativus* L., and *Pisum abyssinicum* A. Braun	Gibberellic acid (GA_3 0.2 g/L)	Enhanced germination percentage, improved shoot and root length, decreased germination time, and improved total weight of crops	Tsegay and Andargie, (2018)
Hordeum vulgare	Hydro-priming, $CaCl_2$ (1.5%), and bio-priming (*Enterobacter* sp.)	Enhanced plant height, grain yield, leaf area, total soluble phenolics and protein, chlorophylls a and b, proline, and glycine betaine and reduced Na+ and MDA contents	Tabassum et al. (2018)
Triticum aestivum	Sodium nitroprusside (SNP 0, 0.1, and 0.2 mM)	Enhanced antioxidant enzymes activities (CAT, POD, and SOD), proline, and total phenolic contents	Q. Ali et al. (2017)
Zea mays	$CaCl_2$ and NaCl (5 g/L)	Increased root and shoot length, germination, number of cobs, number of branches, and seed yield	Gebreegziabher and Qufa, (2017)
Triticum aestivum	$CaCl_2$ (50 mM)	Improved growth, stabilizing cell membranes, enhanced chlorophyll content, promoted nitrate reductase activity, and scavenged ROS activities	Al-Tamimi et al. (2016)
Triticum aestivum	KCl and $CaCl_2$ (100 mM)	Increased activities of antioxidant enzymes (POD, CAT, and APX), enhanced germination, low Na+ content, and high proline and low accumulation of H_2O_2	Islam et al. (2015)
Triticum aestivum	Kinetin, salicylic acid, ascorbate (50 mg/L), and $CaCl_2$ (50 mM)	Reduced Na^+ and Cl^- uptake and improved K^+ uptake in leaves	Afzal et al. (2013)
Triticum aestivum	Ascorbate, salicylic acid, kinetin, and $CaCl_2$ (50 mg/L)	Increased fertile tillers, thousand seed mass, grains spike^{-1}, and grain yield, decreased Na+ and enhanced K+ concentration, and enhanced phenolic, total soluble protein, and protease activities	Jafar et al. (2012)
Oryza sativa	Polyamines (tetramine and spermine)	Reduced oxidative damages, modified osmolytes, antioxidants and photosynthesis system, improved stimulation of antioxidant enzymes, and decreased levels of MDA and H_2O_2	Paul and Roychoudhury, (2016)
Alfalfa	Gibberellic acid (0, 3, 5, and 8 mM)	Enhanced germinating rate of seeds and dry weight of seedling, enhanced antioxidant enzymes activities, and decreased membrane damage and MDA content	Younesi and Moradi, (2014)
Triticum aestivum	Gibberellic acid (100, 150, and 200 mg/L)	Improved grain yield, decreased Na+ content in the root and shoot, improved Ca^{2+} and K+ content in roots, reduced free ABA levels in leaf, and enhanced salicylic acid	Iqbal and Ashraf, (2013)

investigated that seed priming with sodium nitroprusside effectively decreased the negative impact of saline stress-induced oxidative stress and played an essential role due to NO in the enhancement of seed vigor, germination, and initial formation of seedlings. They concluded that seed priming with sodium nitroprusside regulated the antioxidative defense mechanisms, encouraged salt tolerance, and resulted in high biomass and grain yield. The seeds of maize primed with $CaCl_2$ and NaCl took less time for germination than unprimed seeds, and the impact of priming was significant in early growth, seed germination, number of branches, number of cobs, and seed yield (Gebreegziabher and Qufa, 2017).

Al-Tamimi et al. (2016) reported that $CaCl_2$ priming mitigated salt stress in all varieties by enhancing chlorophyll content and growth, stabilizing cell membranes, encouraging nitrate reductase activity, and hindering ROS activities. Seeds primed with KCl and $CaCl_2$ has increased germination, antioxidant enzyme activities (CAT, POD, and APX), enhanced proline accumulation, and reduced the accumulation of H_2O_2 in spring wheat varieties. The method of priming with glycine betaine, vitamin B_{12}, sodium nitroprusside, jasmonate, $CaCl_2$, and KCl) improves the activity of POX, APX, and SOD and decreases MDA and H_2O_2 levels in crops under salinity problems (Sadeghi and Robati, 2015; Keshavarz and Moghadam, 2017). The seed priming with ZNPs, glycine betaine, jasmonate, and 3°C chilling enhances APX, POX, and SOD activity, which is related to enhanced nutrient contents of Ca^{+2}, K^+, Zn, and Mg^{+2} in salt-stressed crops (Alasvandyari et al., 2017; M Iqbal and Ashraf, 2007a). Through inorganic salts, the priming process enhances antioxidant enzyme activities in the germination of seeds and regulates organic substance utilization in various portions of an embryo. Additionally, seed priming with $ZnSO_4$ has improved POD, CAT, and SOD activities as

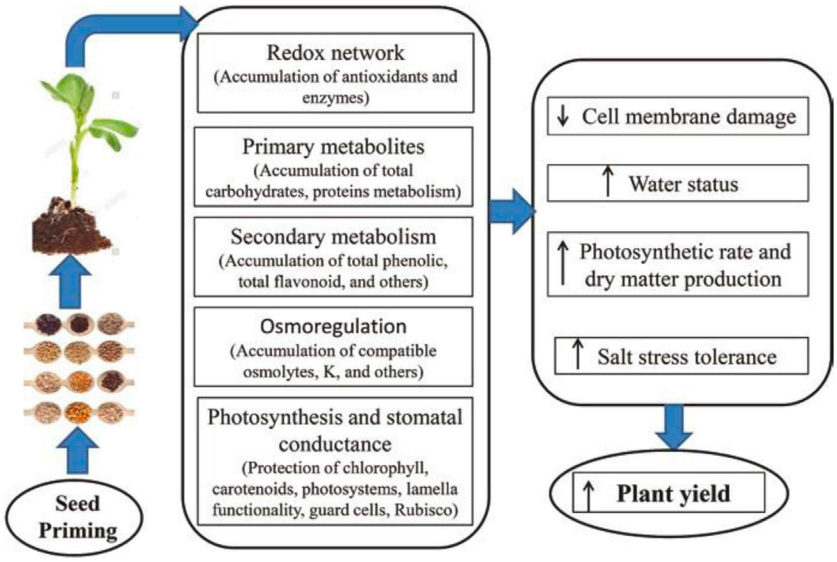

FIGURE 5
Schematic diagram showing the impact of seed priming on physical, chemical, and biological processes (Abdelhamid et al., 2019).

compared with hydropriming (Aboutalebian and Nazari, 2017). Such actions also mitigated stress induced by drought by enhancing the antioxidants in *N. sativa* seedlings (Fallah et al., 2018). Azooz (2009) indicated that the priming of faba bean seeds with SA improved stress tolerance by enhancing POX, APX, CAT, and GR activities. Through seed priming with polyamines, the saline stress tolerance improved rice seedlings by reducing oxidative damage and altering osmolytes, antioxidants, and the photosynthetic system. It also boosted antioxidant enzyme activation and reduced levels of H_2O_2 and MDA (Paul and Roychoudhury, 2017).

A novel mechanism for seed priming modulates molecular, physiologic and biochemical variations

Seed priming enhances rapid and healthy seed growth and vigorous seedling production under saline stress or normal situations. This is due to the priming stimulation of molecular, physiological, and biochemical changes. These alterations consist of cell enlargement and cell division, upsurge in the production of protein, antioxidant enzyme defense system, and stress receptive proteins (e.g., LEA proteins, dehydrins, and heat shock proteins), epigenetic changes, changes in hormone biosynthesis genes, weaken endosperm and its cap, variations in transcriptome and proteome (Jisha et al., 2013; Alam A. et al., 2021; Ahmad et al., 2021). Abdelhamid et al. (2019) proposed a systematic diagram (Figure 5) in which they explained that seed priming improved redox network, primary and secondary metabolism, osmoregulation, photosynthesis and stomatal conductance, photosynthetic rate and dry matter production, enhanced salinity stress tolerance, and finally plant yield. Additionally, seed priming creates minor stress during the drying of the seed-stage, which suppresses radicle protrusion but later permits seeds to struggle with stress treatment (M. Ashraf and Foolad, 2005; Chen and Arora, 2013; Zulfiqar, 2021). Seed priming induces stress and also improves ROS production, while in small amounts, it functions in signaling networks.

A series of biochemical, cellular, physiological, systemic, and molecular changes is triggered by priming, and this increases plant growth in abiotic stress settings (Varier et al., 2010; Gupta and Huang, 2014; El-Sanatawy et al., 2021; Hussain et al., 2022).

The influence of seed priming on molecular variations

Seed priming enhances the uniformity and germination rate through metabolic restoration during osmotic adjustment, imbibition, and stimulation of pre-germinative metabolic developments in seeds. These comprise an impact on DNA processing, initial reserve mobilization, and reparation mechanisms during duplication (E. A. Ibrahim, 2016; Läuchli and Grattan, 2007; Lutts et al., 2016). However, priming also encourages sprouting activities, i.e., reserve mobilization, energy metabolism, respiration, promoting the enlargement of embryo cells, and endosperm weakening (Lal et al., 2018; Sher et al., 2019; Xu et al., 2021).

By repairing DNA pathways, controlling degrading enzymes, catalase, and antioxidant enzymes, producing nucleic acids and proteins, and accumulating sterols and phospholipids, seed priming improves seed germination (Afzal et al., 2013; Kubala et al., 2015a; Paparella et al., 2015). Furthermore, the appropriate development of seedlings from primed seeds might be due to abiotic stress-responsive proteins, increased plasma membrane fluidity, cell division, and elongation (E. A. Ibrahim, 2016). Similarly, the seed priming process encourages specific defense system mechanisms associated with abiotic stress responses. It enhances the heat shock proteins (HSPs), the addition of defensive proteins, and late embryogenesis abundant and stimulates the membrane efflux pumps (Chen and Arora, 2013; Shalaby and El-Messairy, 2018). It also enhances the protein production potential and post-translational modifications, which encourages abiotic stress tolerance (Kubala et al., 2015).

The seed priming process induces the cross-tolerance manifestation in germinating seeds due to enhanced stress tolerance (Chen and Arora, 2013). The method of seed priming that creates abiotic stress tolerance is likely obtained by two separate approaches. During the first approach, priming encourages the pre-germination metabolism processes such as elongation of embryo cells, improvement in the energy metabolic rate, initial mobilization of reserve food in the seed, and weakening of the endosperm (Chen and Arora, 2013; Becerra-Vázquez et al., 2020; Tania et al., 2020), which is responsible for the transformation of inactive seeds to the state of germination and in turn increases germination. Seed priming executes stresses upon seeds due to which radicle protrusion is suppressed but encourages enzyme activation, support stress responses, osmotic adjustment, and cross-tolerance to abiotic stresses in the second approach. These tolerance stress approaches make a “priming memory” in seeds (primed seeds) that could be employed upon the release of stress and facilitate additional stress tolerance (Chen and Arora, 2013; Hussain et al., 2016; E. A. Ibrahim, 2016; Johnson and Puthur, 2021; Marthandan et al., 2020; Tania et al., 2020).

The boosted germination conducted by the seed priming process is linked to the abundance of the protein involved in the tolerance of oxidative stress, removal of dormancy blocks, membrane repair, targeted proteolysis and post-translation processing capacity, development of immature embryos, modification of embryo tissues, and improvement of pre-germination metabolism (Kubala et al., 2015b; Chen et al., 2021). The priming process-induced molecular responses include expression of the gene to produce new RNAs and proteins and the DNA repair mechanism (Varier et al., 2010). The cycle of DNA repair must be maintained at sufficient rates inside the embryo to promote germination (Wojtyla et al., 2016; Sisodia et al., 2018; Mansour et al., 2019; Rhaman et al., 2021; Baig et al., 2022). During imbibition, the triggered DNA repair processes reactivate the cell cycle of embryonic cells and pass through DNA replication that improves germination output, but faulty DNA repair significantly causes cell death (Balestrazzi et al., 2011a; Balestrazzi et al., 2011). Moreover, seed priming activates DNA repair, which is the most important process, and regulates the potential priming advantages (Rajjou et al., 2012; Wojtyla et al., 2016; Rao et al., 2019). Seed priming can enhance germination through the regulation of specific genes (germination-related genes, plant growth-promoting genes, and antioxidants) (Sadeghi and Robati, 2015; Wojtyla et al., 2016; Panuccio et al., 2018).

The effects of seed priming on physiological variations

The mechanism in which plants maintain a sufficient amount of water for growth and germination by collecting compatible solutes is called the osmotic adjustment (Farhoudi, 2011; Farhoudi et al., 2011; Mansour and Ali, 2017). Seed priming encourages vital physiological mechanisms such as osmotic adjustment and ion homeostasis (M. Ashraf and Foolad, 2005; Sheteiwy et al., 2021; Zhang et al., 2019). Furthermore, osmolytes such as soluble sugars, proline, sugar alcohols, glycine betaine, organic acids, and trehalose play an important role in seed germination after seed priming (Abdel Latef and Tran, 2016; M. Ashraf and Foolad, 2005; Jiang et al., 2022). Under stress conditions, these osmolytes play an essential role in defensive and signaling functions (Iqbal and Ashraf, 2007b; Mansour and Ali, 2017; Chen et al., 2022), and such agents formed in primed seeds enhance germination and increase tolerance to subsequent stress environments (Jiménez-Arias et al., 2015; Tan et al., 2022). The addition of these solutes, as well as inorganic ions, reduces the solute potential of the cells, resulting in a potential gradient of water, and thereafter enables water to be absorbed from the adjacent environment, which results in fast seed germination and stimulates metabolic processes before germination (M. Ashraf and Foolad, 2005; E. A. Ibrahim, 2016; Mansour and Ali, 2017). Flowers et al. (2010) stated that excessive toxic ion omission is a physiologically plant adaptive trait to get saline tolerance. Primed seeds encourage salinity tolerance in plants which is credited to increasing osmotic modification and ionic adjustment maintenance with the accumulation of K^+ and Ca^{+2} (Farhoudi, 2011). Primed seeds reduce the toxic accumulation of Na^+ and Cl^- while increasing K^+ and Ca^{+2} and K^+/Na^+ ratios in seedling growth under saline stress conditions (Akram et al., 2010; M. A. Ashraf and Ashraf, 2012; M. Ashraf and Foolad, 2005). Moreover, seed priming strengthens the physiological base (germination) under the high stress conditions, thereby enhancing the growth of plants.

The dynamic uptake of inorganic ions starts the process of osmoregulation in crops. The process of seed priming mitigates the deleterious effects of saline stress on seed germination and healthy development of seedlings that enhances the addition of Ca^{+2} and K^+ and decreases Na^+ and Cl^- accumulation in emerging seedlings (Afzal et al., 2008; Hussain M. I. et al., 2018; Iqbal et al., 2006), causing maximum uptake of water with less osmotic potential (M. Ashraf and Foolad, 2005; M Iqbal and Ashraf, 2007a). The role of K^+ is significant in enzyme activation, in balancing membrane and turgor potential, and in osmotic regulation of cells (Chérel, 2004; Qin et al., 2022). Similarly, calcium also performs vital roles in cell division and elongation, sustains the integrity of the cell wall, adjusts nutrient uptake through the membrane, increases water uptake in crops, and mitigates the deleterious impact of sodium throughout crop growth (Chérel, 2004; Damalas et al., 2019; Mansour et al., 2019).

The effects of seed priming on biochemical variations

Biochemical variations include the enzymatic activities and antioxidant defense induction through seed priming under a high saline stress scenario. The enzymes involved in cell metabolism, such as esterase, acid phosphatase, and glyoxysome enzymes, as well as those involved in the consumption of accumulated reserves (isocitrate lyase and amylases) perform better after the seeds have been primed (Lee and Kim, 2000; Varier et al., 2010; Di Girolamo and Barbanti, 2012). Furthermore, priming enhances antioxidant enzyme activities and addition of non-enzymatic antioxidants (e.g., soluble sugars, GSH, proline, and ASA) (M. Ali et al., 2019; R Farhoudi, 2012; Farhoudi et al., 2011; Fu et al., 2020; Nawaz et al., 2013; Sedghi et al., 2010). These enhancements can further strengthen the defense mechanism by reducing ROS production (e.g., H_2O_2 and O_2) and improving the ROS scavenging during the germination of seeds (Sedghi et al., 2010; Paparella et al., 2015; Banerjee and Roychoudhury, 2018). Seed priming develops the metabolic activities during germination inside the seeds required for breaking the dormancy of seeds, activation of enzymes, protein synthesis and nucleic acids (such as DNA and RNA), transcription and translation, repair mechanisms, germination metabolism, DNA duplication, antioxidant enzyme activities, enhancing the content of ATP and quantity of mitochondria, repairing destroyed seed parts, and reducing leakage of metabolites. Generally, priming motivates sequences of biochemical, metabolic, and physiological changes that are associated with improvement of healthy growth and germination performance and enhance tolerance of abiotic stresses (E. A. Ibrahim, 2016; Tanou et al., 2012; Gao et al., 2021). Compared to normal imbibition, the advantages of seed priming comprise the upregulation of genes and proteins involved in cell elongation and division, translation, mobilization of the reserve, modification of the cell wall, transcription, water transport, and stress oxidative response, as well as membrane and DNA repair (Farooq et al., 2020; Kubala et al., 2015a).

The antioxidant system is the most critical protection system in germinating primed seeds to regulate the addition of reactive oxygen species under abiotic stress (Gupta and Huang, 2014; Paparella et al., 2015; Banerjee and Roychoudhury, 2018). Seed priming encourages the activities of antioxidant enzymes, for e.g., SOD, GR, POX, and CAT, and increases nonenzymatic antioxidant levels (i.e., ascorbic acid). These activities are responsible for hindering reactive oxygen species and seed protection by reduction of hydrogen peroxide and superoxide production (Biosci et al., 2019; E. A. Ibrahim, 2016; Paparella et al., 2015; Sedghi et al., 2010). Furthermore, it encourages the addition of photoprotective pigments (anthocyanin) that increase ROS scavenging and crop protection (Banerjee and Roychoudhury, 2016, 2018; Wang et al., 2022). The addition of MDA decreases with seed priming, which increases with abiotic stress, and is further used as an oxidative stress measure. This decline is related to improved membrane repair of antioxidant enzyme inductive responses during the seed priming process (Bhanuprakash, 2015; Banerjee and Roychoudhury, 2018; Hossain et al., 2020; Zulfiqar, 2021).

Conclusion

From the literature, it is concluded that the process of seed priming with various priming materials could mitigate salinity stress through the development of physiological, biochemical, and morphological mechanisms in germinating seeds, which enhance saline tolerance of different crop seeds to ameliorate salinity. Seed priming enhances antioxidant enzyme activities (APX, POD, SOD, and POX), which helps in the scavenging of ROS such as hydroxyl radicals (-OH) H_2O_2, and superoxide (O_2^-), resulting in better seedling growth and germination. Furthermore, seed priming enhances crops' overall yield by reducing germination time, enhancing germination percentage, germination index, seedling growth, total water content, and photosynthesis activity, and improving saline tolerance of crops under saline stress conditions. Additionally, seed priming also reduces MDA accumulation, which is related to inductive responses of antioxidant enzymes and better membrane repair. The application of seed priming decreases the toxic ion effect by reducing the Na^+ and Cl^- uptake and increasing the K^+ and Ca^{+2} accumulation in developing seedlings. Furthermore, seed priming also encourages photoprotective pigments (anthocyanin) that increase ROS scavenging and crop protection. Various kinds of priming agents have varying properties and effects on different crops.

Future prospects

- Different crop capabilities need to be evaluated under varying saline and environmental conditions.
- Different seed priming chemicals need further exploration for enhanced seed germination and growth and their

evaluation on crop production under saline-stressed environments.

- Different priming methods, including osmopriming, bio-priming, hydro-priming, halo-priming, and hormonal priming, with various priming agents in different proportions need to be studied on different crops under different salinity conditions.
- Rapid seed growth and crop production need to be the utmost duty of scientists to achieve food security goals for humanity in the near future under different adverse environmental conditions.
- Advanced seed priming methods such as priming with nanoparticles and seed priming with physical agents (UV radiation, X-rays, gamma rays, and microwaves) need to be used in order to minimize the salinity stress and finally increase the overall yield of different crops.

Author contributions

Manuscript writing MOK, Supervision and conceptualization MOK, MI, Rewriting and Editing AM, SN, MKK, Proofreading and reviewing IU, MaA. All authors have read and approved this manuscript.

Acknowledgments

The authors express their gratitude to the editorial board and reviewer for their efforts for suggesting and reviewing this work. The authors also appreciate the editor for his cooperation during the review process.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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