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Seed Priming for Mitigating Salinity Stress Effects in Plants: A General Review

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ABSTRACT

Salinity is a significant abiotic stressor that inflicts considerable harm on agricultural fields and plants. Factors such as global warming, improper irrigation practices, excessive fertilization, drainage issues, inappropriate tillage and cultivation methods contribute significantly to the emergence of salinity problems in agricultural lands. When faced with stressors, plants employ various mechanisms to ensure their survival. Consequently, salinity stress adversely affects seed germination, leads to stunted plant growth, reduces yield, results in the accumulation of reactive oxygen species (ROS), diminishes chlorophyll content, elevates proline levels, promotes the production of malondialdehyde (MDA) and impacts osmoprotectants like glycine betaine. Salt stress not only induces osmotic stress and ion toxicity but also disrupts plant nutrient uptake. Today, numerous approaches are available to mitigate the detrimental impacts of stressful conditions and one such method is seed priming, which encompasses various techniques. This review delves into the adverse effects of salinity on plants and examines the role of seed priming processes in ameliorating these harmful consequences.

Key words: Abiotic stress, Priming techniques, Seed germination, Stress resistance.

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Plants face a multitude of stressors throughout their lifecycles, which can originate from both abiotic and biotic sources. Among these challenges, high salinity stands out as a prominent abiotic stressor that poses a significant environmental threat (Jisha *et al*., 2013). Additional abiotic stresses impacting plants include heat, salt, irradiation and light stress, all of which have detrimental effects (Reyes and Cisneros-Zevallos, 2007; Singh *et al*., 2022). Abiotic stresses impose severe limitations on crop production worldwide, exacerbated by global warming, climate fluctuations and unpredictable weather patterns (Deshmukh *et al*., 2017). Notably, soil salinity has emerged as a paramount global concern (Attia *et al*., 2021: Hafeez *et al*., 2021; Mukhopadhyay *et al*., 2021; Hossen *et al*., 2022; El-Beltagi *et al*., 2023; El-Hawary *et al*., 2023). Disturbingly, research indicates that over 33% of agricultural regions are currently grappling with salinity issues (El-Beltagi *et al*., 2023). The rise in salinity within agricultural lands can be attributed to factors such as global warming and inappropriate farming practices (Shrivastava and Kumar, 2015). This salinity stress disproportionately affects many plant species that are crucial for human nutrition, as they exhibit varying degrees of sensitivity or tolerance to salt stress. Consequently, ensuring food security, safe food access and sustainable agriculture for our growing global population becomes an increasingly daunting challenge.

Adverse effects of salt stress on plants

Germination and plant growth

Salinity exerts its influence on all plant processes (Xiong and Zhu, 2002; Johnson and Puthur, 2021; Lini'c *et al*., 2021), resulting in disruptions across various developmental stages, including seed germination, plant growth, development, reproduction and yield (Shrivastava and Kumar, 2015). The adverse effects of salinity on germination and the hampering of plant growth are closely linked to ion toxicity, thereby subjecting plants to stress (Katambe *et al*., 1998). The impact of salt accumulation in soils on plant growth varies across different developmental stages (Bernstein, 1975). While plants can experience salinity stress at all growth stages, germination and the early growth phase are notably more sensitive for the majority of plant species (Ibrahim *et al*., 2018; Ali *et al*., 2020; Ali *et al*., 2021; Dhanyasree *et al*., 2022). Seed germination, a pivotal and delicate stage in plant development, plays a critical role in shaping plant growth, yield and quality (Gupta and Huang, 2014) (Fig 1).

Stomatal conductivity, photosynthesis and carotenoids

High salt concentrations in the soil or water not only hinder the uptake of water through plant roots but also lead to the inhibition of stomatal conductivity, photosynthesis and overall plant growth (Shrivastava and Kumar, 2015; Gürsoy, 2022a; Oliviera *et al*., 2023). The impact of salt stress on

photosynthesis involves a reduction in stomatal conductivity, a critical process that diminishes nutrient and water uptake, ultimately leading to a decrease in chlorophyll content (Ahanger *et al*., 2020). Furthermore, disruptions in stomatal arrangement, attributed to ion imbalances, result in decreased photosynthesis capacity, reduced leaf surface area and a host of related morphological and biochemical disturbances, ultimately diminishing yield and its components (Granaz *et al*., 2022; Hossen *et al*., 2022). Salt stress inflicts damage on plant membranes, alters the activity of plant growth regulators and further suppresses photosynthesis, impacting all physiological processes and potentially leading to plant death (Ibrahim *et al*., 2016). Some studies have reported that carotenoid levels may increase under stress conditions (Gürsoy, 2020; 2022b) (Fig 1).

Plants responses to salt stress

When confronted with stress-induced changes, plants employ a variety of mechanisms for self-protection. One such method involves increasing the production of reactive oxygen species (ROS), which in turn triggers oxidative stress and leads to ion imbalance issues within the cells (Nabi *et al*., 2019). Plants initiate the generation of ROS as an initial response to various abiotic stresses, such as salinity and drought, among others (Fig 1). This response is recognized for its potential to inflict significant damage to cell structures and disrupt normal cellular functions (Deshmukh *et al*., 2017).

Enzyme activities

Plants employ a range of mechanisms to shield themselves from the detrimental effects of ROS. Among these protective strategies is the upregulation of antioxidant enzymes that serve to neutralize the impact of excessive ROS production (Shaki *et al*., 2017) (Fig 1). Some prominent members of these enzymes include superoxide dismutase (SOD), peroxidase (POX) and catalase (CAT), all belonging to the group of enzymatic antioxidants. In addition to enzymatic defenses, plants produce non-enzymatic antioxidants, like phenolic compounds, as a shield against heightened ROS production (Grassmann *et al*., 2002; Zamljen *et al*., 2022). Consequently, the augmentation of antioxidant enzymes and the presence of non-enzymatic phenolic compounds play a vital role in the plant's response mechanism to stress. Furthermore, high salinity stress in plants not only triggers the formation of superoxide but also induces the generation of singlet oxygen, hydroxyl radicals and hydrogen peroxide (Rajput *et al*., 2021).

Malondialdehyde (MDA) and proline

In addition, the excessive intake of sodium ions (Na^+) leads to an ion imbalance within plant cells and results in membrane damage, primarily through the production of malondialdehyde (MDA) and proline (Kishor and Sreenivasulu, 2014; Fang *et al*., 2021; Gürsoy, 2022b). In response to the effects of salt stress, both MDA and proline production increase (Fig 1). MDA, or lipid peroxidation, is recognized as a byproduct of active oxygen species under various stress conditions (Fu and Huang, 2001; Yang *et al*., 2009; Gürsoy, 2022b) and it serves as a natural indicator of oxidative damage induced by salt stress. Meanwhile, proline assumes critical roles in scavenging free radicals during salinity stress (Zhu *et al*., 2019). This versatile compound, proline, ranks among the most commonly encountered osmolytes (Saxena *et al*., 2013).

Seed priming and its beneficial effects

Various techniques have been adapted to enhance plant tolerance to stresses (Jisha *et al*., 2013). Among these methods, seed priming stands out as a low-risk, cost-effective and easily applicable technique that effectively boosts plant resistance to various stressors (Jisha *et al*., 2013; Thakur *et al*., 2019; Garcia *et al*., 2022; Gürsoy, 2022c; Paul *et al*., 2022). Moreover, the priming process is highly efficient in enhancing both seed germination and seedling growth by triggering numerous vital processes (Johnson and Puthur, 2021). Seed priming contributes to stress reduction through various means, including early and uniform

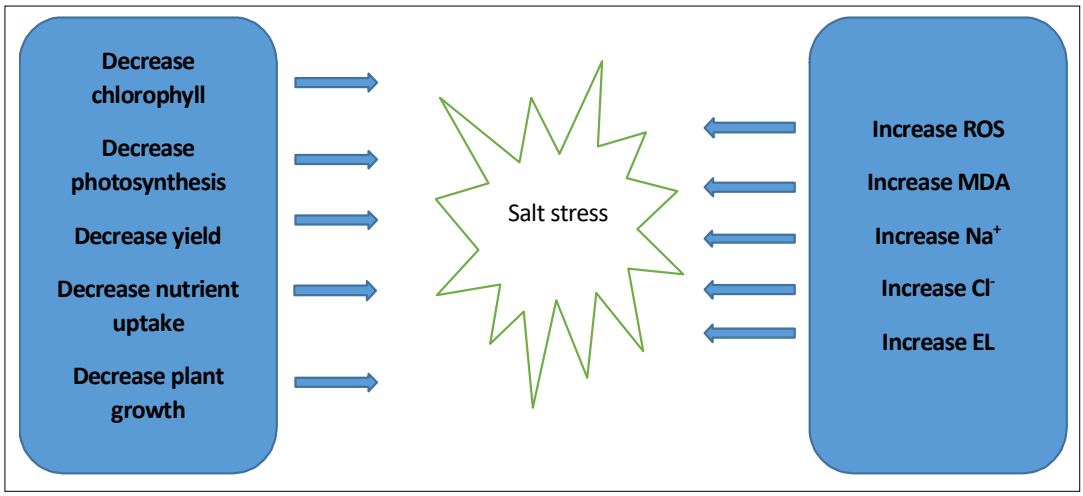


Fig 1: Effects of salt stress on some characteristics of plants.

germination, accelerated root and shoot development and the promotion of overall plant growth (Ghosh and Atta, 2022; Patel *et al*., 2023). It not only ensures consistent and rapid germination but also fortifies resistance against a range of environmental stressors (Afzal *et al*., 2016; Johnson and Puthur, 2021). Priming induces enhanced germination by introducing significant physiological variation in the seed (Damalas *et al*., 2019). Essentially, seed priming involves the initiation of diverse processes in plants through the treatment with natural and synthetic compounds (Jisha *et al*., 2013) and these applications enhance various characteristics along with cellular and plant development (Savvides *et al*., 2016). Numerous studies have explored the effects of priming applications against one or more stress factors (Savvides *et al*., 2016; Van Oosten *et al*., 2017).

Priming methods

Various priming techniques are available to reduce the effects of stress factors which includes hydropriming, halopriming, osmopriming, hormonal priming and biopriming (Neto *et al*., 2020; Chakraborty and Dwivedi, 2021).

Hydropriming

One of the most widely employed priming techniques in recent times is hydropriming. Hydropriming is an environmentally friendly, cost-effective and easily applicable method for stress protection (Forti *et al*., 2020; Garcia *et al*., 2022) (Fig 2). Essentially, hydropriming involves soaking seeds in pure water for a specified duration, subject to specific light and temperature conditions (Zhao *et al*., 2018; Damalas *et al*., 2019; Tanwar *et al*., 2023). This approach has been shown to have positive effects on plant growth, both during the initial stages and later in development (Rhaman *et al*., 2020). Hydropriming is particularly valuable for crops where germination and growth may be hampered by stressful conditions (Castro-Colina *et al*., 2012). The application of hydropriming has a significant impact on the antioxidant system of plants under various stress conditions. For instance, in a study involving alfalfa seeds subjected to salt stress conditions, Amooaghaie (2011) observed an increase in the activity of various enzymes following hydropriming. Concurrently, proline content, electrolyte leakage (EL) and malondialdehyde (MDA) levels decreased. Similarly, when hydropriming was applied to *Quercus rugosa* seeds, rapid and synchronized germination and improved growth parameters were observed (Castro-Colina *et al*., 2012). In the case of corn seeds exposed to salt stress, hydropriming positively affected germination and seedling growth parameters (Jayesh and Meeta, 2015). Moreover, hydropriming has been found to enhance photosynthetic activity, stomatal conductivity and evapotranspiration in bread wheat seeds under both normal and stress conditions (Tabassum *et al*., 2017). Researchers have also reported that hydropriming can increase the salt tolerance of sunflower plants, with no accumulation of proline in hydroprimed seedlings, indicating protective properties (Matias *et al*., 2018). In rice seeds, hydropriming has had a positive impact on morphological and physiological properties (Mondal *et al*., 2018), while in faba bean seeds, it has improved germination parameters and seedling emergence (Damalas *et al*., 2019). An increase in chlorophyll content has been observed after hydropriming (Bourioug *et al*., 2020). Furthermore, in *Medicago truncatula* seeds, hydropriming resulted in the best germination outcomes (Forti *et al*., 2020). In the context of enhancing resistance to *Aspergillus niger* in wheat plants, various priming treatments were applied, with hydropriming proving to be particularly effective. Physiological and biochemical properties of wheat demonstrated that hydropriming was more effective in disease reduction and it led to higher expression levels of β-1,3-glucanase, Thaumatin-like protein (TLP) and chitinase, further contributing to increased disease resistance (Gul *et al*., 2022). Additionally, a 6-hour hydropriming treatment was found to be highly effective in increasing the germination of rice cultivars (Ranmeechai *et al*., 2022).

Halopriming

Halopriming is another commonly employed technique, wherein seeds are primed in a solution containing organic salts. This method expedites germination and fosters uniform seedling growth even under the influence of stress factors (Afzal *et al*., 2008; Hidayah *et al*., 2022). Halopriming has been demonstrated to offer numerous advantages, including improved crop establishment, enhanced uniformity, increased plant growth and higher productivity, particularly in the face of abiotic environmental stresses, which are essential to meet future food demand sustainably and reliably (El-Sanatawy *et al*., 2021). When seeds undergo halopriming, it can bolster plant growth even in the presence of salt stress conditions (Hidayah *et al*., 2022). It achieves this by regulating the activities of existing enzymes and producing essential germination metabolites (Ahmad *et al*., 2017). For instance, research conducted with wheat seeds treated with different inorganic salts ($CaCl_2$, NaCl and $CaSO_4$) found that halopriming enhanced salt stress tolerance and improved germination, seedling growth parameters, seedling vigor, ion homeostasis and starch metabolism (Afzal *et al*., 2008). Halopriming also helps prevent the accumulation of sodium ions (Na^+) through tissue tolerance effects. Additionally, halopriming contributes to enhanced plant and seedling growth and increases salinity tolerance, especially during the seedling stage (Hidayah *et al*., 2022). Halopriming plays a pivotal role in regulating enzyme activities, ensuring the production of necessary germination metabolites (Ahmad *et al*., 2017). In the case of rice seeds, priming under salt stress conditions stimulated metabolism and increased seedling vigor (Jisha and Puthur, 2014). Furthermore, when halopriming treatment was applied to *Gerbera jamesonii* and *Zinnia elegans* seeds with $CaCl_2$, KNO_3 and KCl, it resulted in uniform maturity and improved flower harvesting (El-Sanatawy *et al*., 2021). In a study that examined the effects of halopriming in conjunction with different irrigation systems on corn seeds, researchers found that it enhanced germination uniformity, speed, rate and

strength. Additionally, it increased water use efficiency in field conditions compared to the control, which was significant in mitigating the adverse effects of water scarcity (El-Sanatawy *et al*., 2021). Halopriming has also been applied to *Hibiscus sabdariffa* seeds under salt stress conditions, leading to an increased germination rate and emergence percentage (Taghvaei *et al*., 2022).

Osmopriming

Osmopriming involves the immersion of seeds in various osmotic solutions, such as polyethylene glycol, mannitol, sorbitol and more (Ghassemi-Golezani *et al*., 2008; Garcia *et al*., 2022). This technique can enhance seed resistance to salt stress (Fig 2). When seeds are exposed to osmotic solutions, it promotes the expression of numerous stress-related genes and proteins, expediting stress and cross-tolerance mechanisms (Benadjaoud *et al*., 2022). Osmopriming operates by facilitating the movement of components within seeds at low water content, enabling seeds to slowly take up water while reducing cell damage (Garcia *et al*., 2022). This process activates stress tolerance mechanisms, including enhanced antioxidant capacity and the activation of signaling molecules, ultimately leading to higher productivity (Kerchev *et al*., 2020; Stasio *et al*., 2020). Osmopriming induces molecular changes in seeds, consequently enhancing seed germination and emergence across a wide range of plant species (Hassanpouraghdam *et al*., 2009). For instance, maize seeds subjected to osmopriming exhibited improved germination and vigor characteristics (Ghiyasi *et al*., 2011). The effects of osmopriming on rapeseed varieties were examined, revealing higher germination percentages, increased radicle and seedling height, greater dry weight and higher sodium (Na) content in primed seeds compared to unprimed seeds. Notably, potassium (K) content in primed seeds was also relatively higher than in unprimed seeds (Hassanpouraghdam *et al*., 2009). In another study involving soybean seeds treated with polyethylene glycol (PEG 6000), the application of osmopriming at -1.2 MPa for 12 hours yielded the most favorable results across the examined properties. Primed seeds generally exhibited better characteristics than the control group (Sadeghi *et al*., 2011). Osmopriming has been found to enhance seed germination and seedling growth in barley (Tabatabaei, 2013). Additionally, when osmopriming was applied to rapeseed seeds using polyethylene glycol, transcription factors, small interfering RNA, hormones and germination properties all showed positive effects (Kubala *et al*., 2015). Furthermore, the application of osmopriming to *Lavandula stoechas* L. plant seeds under salt and water stress conditions effectively mitigated the adverse effects of stress on germination (Benadjaoud *et al*., 2022).

Hormonal priming

Hormonal priming is a priming technique that involves the use of various plant growth regulators (Bryksová *et al*., 2020) or phytohormones to stimulate seed metabolism, subsequently promoting plant growth and ultimately increasing yield (Bryksová *et al*., 2020). Plant growth regulators and phytohormones like gibberellins, cytokinins, auxins and salicylic acid are commonly employed to enhance germination and plant growth, especially under stress conditions (Gürsoy, 2019; 2022a). For example, applying kinetin to *Salvia officinalis* seeds under salt stress conditions was found to be effective in mitigating the stress effects (Tounekti *et al*., 2011). In a study examining salt tolerance in wheat seeds primed with gibberellic acid, positive effects were observed on seed yield, salt tolerance, ion uptake in roots and seedlings Iqbal and Ashraf (2013). Gibberellic acid applied to oat varieties under salt stress conditions resulted in increased germination percentages, shoot and root length, total weight and water content parameters, effectively alleviating the negative effects of stress (Chauhan *et al*., 2019). Hormopriming with gibberellic acid positively affected the germination properties of safflower varieties (Gürsoy, 2019). When salicylic acid (SA) was applied from the leaf under saline conditions, it positively

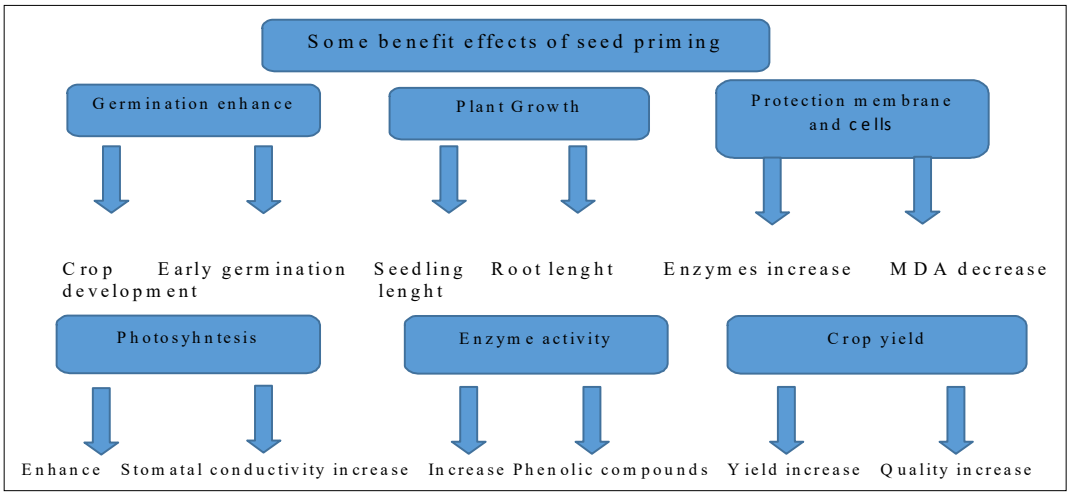


Fig 2: Effects of priming applications under salt stress conditions.

affected plant height, stem diameter and chlorophyll content (Rehman *et al*., 2019). Additionally, in lentil seeds, both hydropriming and osmopriming applications were found to improve seed germination and seedling growth (Ghassemi-Golezani *et al*., 2008). Wheat seeds primed with kinetin and gibberellic acid under salt stress conditions displayed interesting outcomes. Gibberellic acid increased K^+ levels and decreased the accumulation of Na^+ and Cl^- in seedlings, whereas kinetin increased Cl^- accumulation and decreased K^+ accumulation (Akhtar *et al*., 2021). Hormopriming with salicylic acid had positive effects on the morphological and biochemical properties of sunflower and linseed seeds under salt stress conditions Gürsoy (2022a). Furthermore, the application of salicylic acid to the seeds of the *Ocimum basilicum* plant under salt stress was effective in mitigating the adverse effects of stress on gas exchange and total chlorophyll parameters (Silva *et al*., 2022).

Biopriming

Biopriming is a seed priming technique involving the inoculation of seeds with living bacteria, including plant growth-promoting rhizobacteria (Mahmood *et al*., 2016). It typically entails soaking seeds in solutions containing beneficial bacteria for specific durations (Abuamsha *et al*., 2011). This environmentally friendly method can be applied to all plants (Deshmukh *et al*., 2020; Miljakovi´c *et al*., 2022) and serves to reduce the transmission of pathogens to both the seeds and the soil by coating the seeds with beneficial microorganisms (Forti *et al*., 2020). Beneficial microorganisms used in biopriming include *Bacillus* spp., *Pseudomonas* spp. and *Trichoderma* spp. (Paparella *et al*., 2015). Biopriming offers a means to protect seeds from bacterial damage and enhance their resistance to various biotic and abiotic stresses (Rajendra Prasad *et al*., 2016; Miljakovi´c *et al*., 2022). For instance, biopriming of chickpea seeds demonstrated significant improvements in disease control and yield compared to untreated seeds (Parmar *et al*., 2021). Soaking pigeonpea seeds in liquid cultures, such as pink-pigmented facultative methylotroph (PPFM) at a 1:100 dilution for 3 hours or *Rhizobium* or phosphobacteria at a 1:50 dilution for 4 hours, increased germination and seed vigor (Raja *et al*., 2019). While the populations of *Rhizobium* and phosphobacteria in microbial-infused seeds showed only slight reductions during three months of storage, the population of PPFM decreased significantly. Nevertheless, PPFM exhibited better seed quality enhancement among the cultures. A consortium of *Rhizobium* and PPFM at a 1:1 ratio for 3 hours increased seed vigor with improved microbial populations (Raja *et al*., 2019). Biopriming with *Bacillus* spp. applied to *Medicago truncatula* seeds resulted in increased seedling growth and biomass (Forti *et al*., 2020). Seed germination and seedling development were also positively affected. In another study, biopriming with *Pseudomonas geniculata* was applied to corn seeds in salty sodic soil, leading to the mitigation of salt-induced damage, enhanced plant growth and reduced crop losses. This application of *P. geniculata* reduced the uptake of sodium ions (Na^+) while increasing potassium (K^+) and calcium ions (Ca^{2+}) in maize roots, maintaining ionic balance and homeostasis under excessive salt conditions (Singh *et al*., 2020). Additionally, biopriming with a commercial biostimulant and plant growth-promoting rhizobacteria (PGPR) in *Abelmoschus esculentus* genotypes increased plant development, yield and biochemical parameters (Makhaye *et al*., 2021). Furthermore, soybean seeds primed with *Bradyrhizobium japonicum* and *Bacillus megaterium* exhibited improvements in seedling height, seedling vigor, seedling and root weight and germination in both old and normal seeds under stress conditions (Miljakovi´c *et al*., 2022).

Conclusion

Seed priming is a valuable technique that ensures improved germination, seedling and root development, ultimately leading to increased yield and quality of crops. Additionally, it serves as a means to enhance resistance against abiotic stresses. A wide range of priming techniques has been thoroughly researched across various plant species and stress conditions, consistently demonstrating their beneficial effects. Seed priming methods stand out as the optimal solution for promoting germination and seedling development, especially in unfavorable environmental conditions, while also enhancing the plant's defense mechanisms, yield and quality. Seed priming techniques offer several advantages, including cost-effectiveness, ease of application, reliability and environmental friendliness. Consequently, seed priming technology emerges as a highly useful approach to bolster crop production and improve crop quality, particularly under stress conditions.

Conflict of interest

The author have no conflict of interest.

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