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Chapter

Effects of Salinity on Seed Germination and Early Seedling Stage

Cüneyt Uçarlı

Abstract

Salinity is the major environmental stress source that restricts on agricultural productivity and sustainability in arid and semiarid regions by a reduction in the germination rate and a delay in the initiation of germination and subsequent seedling establishment. Salt negatively effects the crop production worldwide. Because most of the cultivated plants are salt-sensitive glycophytes. Salt stress affects the seed germination and seedling establishment through osmotic stress, ion toxicity, and oxidative stress. Salinity may adversely influence seed germination by decreasing the amounts of seed germination stimulants such as GAs, enhancing ABA amounts, and altering membrane permeability and water behavior in the seed. Rapid seed germination and subsequent seedling establishment are important factors affecting crop production under salinity conditions. Seed priming is one of the useful physiological approaches for adaptation of glycophyte species to saline conditions during germination and subsequent seedling establishment. In seed priming, seeds are exposed to an eliciting solution for a certain period that allows partial hydration without radicle protrusion. Seed priming is a simple, low cost, and powerful biotechnological tool used to overcome the salinity problem in agricultural lands.

Keywords: salinity, germination, glycophyte, halophyte, seed priming, plant hormones

1. Introduction

Seed dormancy and germination are distinct physiological processes, and the transition from dormancy to germination is not only a critical developmental step in the life cycle of higher plants but also determines the failure or success of the subsequent seedling establishment and plant growth [1]. Seed germination begins with the water uptake of dry seed (imbibition) and ends with radicle protrusion. Seed germination is affected by adverse environmental conditions including salinity, high temperature, and drought [2].

It is estimated that about approximately 7% of world land is affected by salinity and approximately 20% of 230 million ha irrigated land is salt-affected [3]. This number could be increased in the future due to increased land salinization as a consequence of contaminated artificial irrigation, climate change, and unsuitable land management. Salinity is a major stress responsible for the inhibition of seed germination or reduction in germination percentage and a delay in germination

time in crops. At present, around 30 crop plants provide 90% of plant-based human food and the majority of these crops are not salt tolerant, even salt-sensitive, called glycophytes [4]. There have been high yield losses in these crops under moderate salinity (EC 4–8 dS m^{-1}, approximately 40–80 mM NaCl) [5].

High salinity leads a decrease in osmotic potential of ambient soil water, resulting with a decrease in water uptake by dry seeds (imbibition). Besides, the absorption of excess Na^+ and Cl^- ions from soils creates ionic stress and cause toxicity which contributing to disruption in biochemical processes including nucleic and protein metabolism, energy production, and respiration [6]. Salinity also damages the nutrient and hormone balances, especially gibberellin (GA)/abscisic acid (ABA), during germination. As a result, high salinity level causes a delay in germination, even inhibition of seed germination depending on salt tolerance of plants. Dynamic balance between the generation and scavenging of reactive oxygen species (ROS) such as hydroxyl radicals, superoxide, and hydrogen peroxide could be disturbed by high salinity stress. ROS damage the macromolecules including proteins, carbohydrates, nucleic acids, and lipids, or cellular structures like membranes, resulting with inhibition of seed germination [7].

Germination has been found to be under strict regulation of plant hormones, especially GA and ABA [8]. ABA promotes seed dormancy and inhibits germination of seed, whereas GAs release dormancy and stimulate germination. Plant hormones ethylene (ET), and brassinosteroids (BRs) also have positive effect on seed germination by controlling the inhibitory effects of ABA on germination and rupturing testa and endosperm [9, 10]. The plant hormones widely took part in determining the physiological state of a seed and regulating the germination process by interacting each other [11]. Hormones are regulated by distinct transcription factors and signaling components including NO and H_2O_2, showing the complexity of seed germination regulation. While some plant genes control the activity of plant hormones, and the other plant genes are activated by plant hormones [10]. Signaling molecules, such as NO and H_2O_2, also promotes germination and reduce the dormancy by enhancing ABA catabolism and GA biosynthesis [12].

Rapid seed germination and subsequent seedling establishment are important factors determining crop production and yield under salinity stress. One of the useful physiological approaches for glycophytes to adapt saline condition is seed priming [7]. Seed priming is an easy, low cost and low risk technique. The seeds are hydrated in specific solutions including plant hormones (GA3, ET, auxins, kinetin), antioxidant compounds (ascorbic acid, glutathione, tocopherone) organic solutes (proline, glycine betaine), inorganic salts (KNO_3, $CaCl_2$, and KCl), and particular bacteria and fungi species for a certain time to allow metabolic process of germination, followed by drying the seed to inhibit occurring of radicle protrusion [13].

2. Soil salinity and salinity stress

Plants, being sessile nature, are simultaneously subjected to various adverse conditions including salinity, drought, cold, heat, excess water, and heavy metals, which limit their development and growth. Salinity is the major environmental stress source that restricts on agricultural productivity and sustainability in arid and semiarid regions [14]. Salinity is a global issue that affects about 7% of the world's total land area, including 20% total cultivated lands and 33% of irrigated land, causing estimated yield losses of 20% worldwide [15, 16]. Besides, it is estimated that every year 10 million ha of agricultural land destroyed by salinized soil [17]. This rate can be increased by global climate change, use of contaminated irrigation water, intensive farming and poor drainage [18–56]. Without proper and

sustainable control, salinity-affected areas will increase to more than 50% of the world's total arable land by 2050 [15]. This rate can be accelerated by increase in sea water level by climate change, excessive use of groundwater for irrigation, increasing use of low-quality water for irrigation and massive introduction of irrigation associated with intensive farming and poor drainage [57].

Soil salinity is a measure of the concentration of all the soluble salts in soil water, and is usually expressed as electrical conductivity (EC) of the saturation extract (ECe) with units of deci siemens per meter (1 dS m^{-1}) [58]. The soils were classified as saline, sodic or saline-sodic based on the total concentration of salt and the ratio of Na^+ to Ca^{2+} and Mg^{2+} in the saturated extract of the soil [59]. When the ECe exceeds 4 dS m^{-1} (approximately 40 mM/L NaCl) and exchangeable sodium percentage is less than 15 with sodium adsorption ratio (SAR) < 13, the soil is saline. The major problem with saline soils is the presence of soluble salts, primarily Cl^-, SO_4^{2-}, and sometimes NO_3^-. The pH of saline soils is usually below 8.5. Sodic (alkali) soils have an ECe < 4 dS m^{-1}, ESP > 15, and SAR > 13. Therefore, Na^+ is the major problem in these soils. Sodic soils have a pH between 8.5 and 10. Saline-sodic soils have an ECe > 4 dS m^{-1}, SAR > 13, and an ESP > 15. Thus, both soluble salts and exchangeable Na^+ are high in these soils. Saline-sodic soils have similar salt and pH levels as saline soils. USSL Staff [59] has described the general relationship of ECe and plant growth as the following:

- non-saline (ECe ≤ 2 dS m^{-1}): salinity effects mostly negligible;
- very slightly saline (ECe = 2–4 dS m^{-1}): yields of very sensitive crops may be restricted;
- slightly saline (ECe = 4–8 dS m^{-1}): yields of many crops are restricted;
- moderately saline (ECe = 8–16 dS m^{-1}): only salt tolerant crops yield satisfactorily; and
- strongly saline (ECe ≥ 16 dS m^{-1}): only a few very salt tolerant crops yield satisfactorily.

3. Seed germination

Seed germination is a complex multi-stage developmental process and regulated by internal and external factors. Internal factors include proteins, plant hormones (gibberellins/ABA balance, ethylene, and auxin), chromatin-related factors such as methylation, acetylation, histone ubiquitination, related genes (maturating genes and hormonal and epigenetics-regulating genes), non-enzymatic processes, seed age, seed size, and structural components of seed including (endosperm and seed coat). Besides, external factors containing moisture, light, salinity, temperature, acidity, and nutrient also affect the seed germination [60, 61].

Seed germination begins with imbibition, the uptake of water by the dry mature seed, and ends with visible protrusion of radicle through testa [62]. Successful germination requires optimum environmental conditions, including water, oxygen, and temperature to initiate this process. Germination/sprouting is regulated by plant hormones such as gibberellic acid (GA), abscisic acid (ABA), ethylene, auxins, cytokinins, and brassinosteroids [63]. Among them, ABA and GA are two important regulators, which play antagonistic roles in seed dormancy and germination [64].

The process of seed germination can be divided into three phases (**Figure 1**) [65]. Phase I begins with imbibition of dry seeds and ends with the early plateau phase of water uptake. Phase II includes reactivation of metabolisms, significant induction of hormonal and enzyme activity using surviving structures and components in the desiccated cells, genes involved in amino acid and nucleic acid synthesis, restarting of cellular respiration with genesis of mitochondria, mobilization of reserved, RNA and protein synthesis machinery [66, 67]. Phase III is post-germination stage involves establishment of seedling and the induction of genes for photosynthetic metabolism after radicle cells elongate and divide [68].

Gibberellins and ABA are two key phytohormones regulating seed germination and seedling growth [69]. While GA breaks dormancy and enhances the seed germination and seedling, ABA inhibits germination and enhances seed dormancy [10]. However, the ratio of the two hormones, rather than the absolute level of each hormone, plays a key role in regulating the breaking of seed dormancy and the onset of germination [70]. GA/ABA balance determines fate of the seed; germination or dormancy. Gibberellins induce the synthesis and production of α-amylase, proteases, and β-glucanases, resulting in the germination of seeds [71]. GAs also stimulate the genes involved in weakening of endosperm and expansion of embryo cell [10]. On the other hand, ABA suppresses expression of many hydrolytic enzyme genes to prevent viviparous germination and inhibits promoting effect of GA on radicle growth and embryo expansion by inhibiting water uptake and hence cell-wall loosening, which is a key step to start germination [72].

Ethylene is a gaseous hormone involved in various processes, including positive regulation of seed germination. Ethylene breaks the primary and secondary dormancy and promotes seed germination by reducing ABA levels or sensitivity [73]. Brassinosteroids (BRs) and auxin induce the secretion of ethylene which works in conjunction with GAs to induce germination [10]. Auxins reduce seed sensitivity to ABA by overexpressing microRNAs and interacting with GAs to counteract ABA suppression during germination [74, 75].

Low temperature decreases seed dormancy and enhances germination in many species, while high temperature has the negative effect on germination and induces secondary dormancy [70]. High temperature down-regulates the genes involved in synthesis of GA synthesis and deactivation of ABA, whereas genes involved in ABA synthesis are up-regulated by high temperature. Therefore, transcriptional changes in ABA and GA metabolism and signal pathways results with inhibition of germination or a delay in germination [76]. Light has been considered both to stimulate

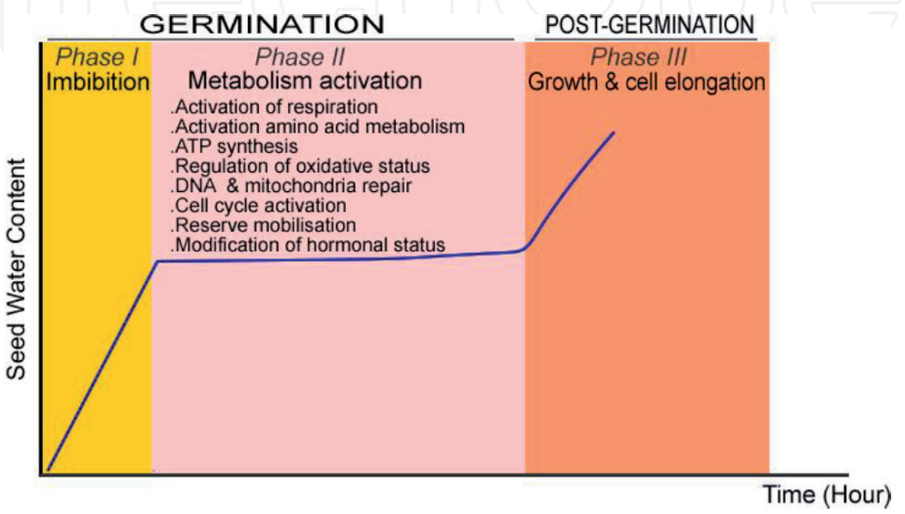


Figure 1.
Major events associated with germination and subsequent post-germinative growth (based on [13, 65]).

germination and to terminate dormancy by increasing the expression of GA anabolic genes, GA3ox1 and GA3ox2, and repressing expression of GA catabolism gene GA2ox2 [77].

In addition to phytohormones, several signal molecules, including as nitric oxide (NO) and reactive oxygen species (ROS), also regulate seed dormancy and germination [68]. ROS is an important regulator during seed germination because of the interaction with lipids, DNA, and protein molecules, as well as phytohormones including ABA and GA in the cell [78]. The biochemical and cellular reactions stimulated by water uptake are accompanied by the generation of ROS [79]. Hydrogen peroxide (H_2O_2) serves as a signaling hub for the regulation of seed dormancy and germination; the accurate regulation of H_2O_2 accumulation by the cell antioxidant mechanism is important to achieve a balance between oxidative signaling that enhances germination and oxidative damage that inhibits germination or delays in germination time [80]. N compounds, including NO, promotes seed germination through increasing amylase activities, adjusting K^+/Na^+ balance, and enhancing seed respiration and ATP production [81].

4. Effect of salinity on seed germination and early seedling stage

Salinity affects seed germination process through osmotic stress, ion-specific effects and oxidative stress, shown by decreasing germination rate and extended germination time [82]. Salinity increases external osmotic potential that reduces water uptake during imbibition [83]. Salinity may affect the germination of seeds by the toxic effects of excess sodium and chloride ions on embryo viability [84, 85]. The toxic effects include disruption to the structure of enzymes and other macromolecules, damage to cell organelles and the plasma membrane, the disruption of respiration, photosynthesis and protein synthesis [85–87].

In general, seed germination progresses in three phases under normal conditions. Seed germination begins with the rapid water uptake by dry seed (imbibition) (Phase I). A plateau phase, known as phase II, follows this phase. The cellular metabolisms are reactivated, and water uptake is restricted in phase II. This is followed by phase III, a post-germination phase, which is characterized by continuous water uptake until germination is complete (**Figure 1**). Based on these three phases, the inhibition of seed germination or delaying in germination time under salinity stress may be generally ascribed to osmotic stress in the phase I and ionic stress in the phase II. Osmotic stress and ionic stress interact together to inhibit or delay germination of seed during the phase III [88].

Salinity may adversely influence seed germination by decreasing the amounts of seed germination stimulants such as GAs, enhancing ABA amounts, and altering membrane permeability and water behavior in the seed [89]. In higher plants, salinity has been demonstrated to change expression profiles of the genes encoding GA metabolic enzymes, including copalyl diphosphate synthase (CPS), ent-kaurene synthase (KS), ent-kaurene oxidase (KO), ent-kaurenoic acid oxidase (KOA), GA 20-oxidase (GA20ox), GA 3-oxidase (GA3ox) and GA 2-oxidase (GA2ox), resulting with change in endogenous GA levels during germination [12].

The germination of seeds is characterized by transcriptional induction of hydrolytic enzymes such as α-amylase [90]. The α-amylase is excreted into the endosperm to break the stored starch to metabolizable sugars that provide ready energy and nutrients for the growing embryo and radicle. Salinity stress may have much effect on delayed germination time than on final germination percentage for most crops. A delay of water uptake and a decrease in the activity of α-amylase with an increase in the concentration of NaCl may be main reasons for delaying of the germination time [91].

The decrease in the α-amylase activity have been reported to be higher in the salt-sensitive genotypes than in the salt-tolerant genotypes. This reduction in the α-amylase activity results with a significant reduction in the translocation of sugars, essential for the developing embryo. Besides, decreasing sugar concentrations also change the osmotic potential of growing cells, resulting in a decrease in water uptake [88].

Both osmotic and ionic effects of salt stress leads to generation of excess reactive oxygen species (ROS) and oxidative damage, which disrupts proteins, lipids, and nucleic acids or the cellular structure including lipid membrane [83].

Plants can be divided into two main groups based on their response to saline stress; salt-tolerant halophytes and salt-sensitive glycophytes (non-halophytes) [6]. The halophytes are plants that are able to grow in the presence of high salt concentrations that generate a low water potential of the soil and kill 99% of other

Plant species	*Maximum salt tolerance	Salt tolerance type	Reference
Salicornia herbacea	1.7 M NaCl	Halophyte	[93]
Suaeda aralocapsica	1.5 M NaCl	Halophyte	[94]
Limonium vulgare	1.5 M NaCl	Halophyte	[95]
Sarcocornia perennis	1.3 M NaCl	Halophyte	[96]
Haloxylon ammodendron	1.3 M NaCl	Halophyte	[97]
Kochia scoparia	1.0 M NaCl	Halophyte	[98]
Kochia prostrata	0.85 M NaCl	Halophyte	[99]
Haloxylon salicornicum	0.8 M NaCl	Halophyte	[100]
Prosopis juliflora	0.6 M NaCl	Halophyte	[100]
Limonium mansanetianum	0.5 M NaCl	Halophyte	[101]
Limonium stocksi	0.4 M NaCl	Halophyte	[102]
Limonium lilacinum	0.3 M NaCl	Halophyte	[103]
Tanacetum cinerariifolium	0.26 M NaCl	Halophyte	[104]
Quinoa (*Chenopodium quinoa* Willd.)	0.3 M NaCl	Halophyte	[105]
Barley (*Hordeum vulgare* L.).	0.25 M NaCl	Glycophyte	[106]
Maize (Zea mays)	0.24 M NaCl	Glycophyte	[107]
Chicory (*Cichorium intybus* L.)	0.21 M NaCl	Glycophyte	[108]
Lentil (*Lens culinaris* Medik.)	0.2 M NaCl	Glycophyte	[14]
Brassica napus	0.2 M NaCl	Glycophyte	[109]
Peanut (*Arachis hypogaea*)	0.2 M NaCl	Glycophyte	[110]
Rice (*Oryza sativa*)	0.16 M NaCl	Glycophyte	[111]
Fig (*Ficus carica* L.)	0.17 M NaCl	Glycophyte	[112]
Button grass (*Dactyloctenium radulans*)	0.1 M NaCl	Glycophyte	[113]
Sorghum (*Sorghum bicolor* Moench)	0.1 M NaCl	Glycophyte	[114]
Ryegrass (*Lolium rigidum*)	0.1 M NaCl	Glycophyte	[115]
Chickpea (*Cicer arietinum* L.)	0.09 M NaCl	Glycophyte	[116]
Tomato (*Solanum lycopersicum*)	0.05 M NaCl	Glycophyte	[117]

Maximum NaCl concentration at which seed germination percentage reduced to 10–20%.

Table 1.
Maximum salt tolerance of halophytes and glycophytes at the germination stage.

species. They are adapted to survive and complete their life cycle under saline levels of higher than 200 mM NaCl. However, seed germination was also affected under salt stress and germination percentage was reduced to less than 10% under 1.7 M NaCl [92, 93]. In halophytes, maximum salt tolerance for seed germination has been reported to vary from 1.7 to 0.26 M NaCl depending on halophyte species and other environment conditions such as temperature, moisture, and light (**Table 1**).

A majority of the common crops, such as tomato, bean, rice, corn, etc., are salinity sensitive or even hypersensitive and they are described as glycophytes [5]. The glycophytes contain 99% of the world's flora and are susceptible to even low levels of salinity (ECe < 4 dS m^{-1}, approximately 40 mM NaCl) [92]. Under conditions of moderate salinity (EC 4–8 dS m^{-1}), all important glycophytic crops reduce average yields by 50–80% [118]. Seed germination in glycophytes is severely inhibited under salinity due to both osmotic stress and ionic toxicity stress, while halophytes are less affected by osmotic stress during germination [12].

5. Alleviation salinity stress on germination by seed priming

Most crops are highly susceptible to saline soil, even when soil has electrical conductivity (ECe) as low as 3 dS m^{-1} [119]. Therefore, salinity stress appears to be a major limitation factor for crop productivity. Seed germination and seedling establishments are the two critical stages in plant growth. These stages are the most sensitive to environmental conditions including salinity [120]. Plants are usually seeded within the top layer of the soil which is more saline than lower layers [121]. Salinity stress may delay or prevent germination of germination of high quality seeds, resulting with crop loss. Rapid seed germination and subsequent seedling establishment are important factors affecting crop production under salinity conditions. Therefore, to decrease the negative effects of salinity stress on seed germination, it is important to know to what extent the genotypic variation in the water uptake pattern during these phases is associated with the salt tolerance of genotypes at the germination stage.

Seed priming is one of the useful physiological approaches for adaptation of glycophyte species to saline conditions during germination and subsequent seedling establishment. Seed priming is a simple, low cost and powerful biotechnological tool used to overcome the salinity problem by promoting seed germination and seedling establishment in agricultural lands [122]. Seed are exposed to an eliciting solution for a constant period that allows partial hydration, but radicle emergence does not occur by re-drying of seed. Seed germination occurs three distinct phases: (i) imbibition, (ii) lag phase (reactivation of metabolisms) and (iii) protrusion of the radicle through the testa. The goal of seed priming is to extend the lag phase, which allows pre-germinative physiological and biochemical processes, but prevent the seed transition towards full germination [123]. Enhanced and uniformed germination of primed seeds occurs by reduction in the lag time of imbibition, activation of enzyme involved in seed germination, initiation of biochemical mechanisms of cell repair, increase in the RNA content and DNA replication, decrease in ROS and lipid peroxidation with increased activity of antioxidant enzymes including as superoxide dismutase, catalase, and glutathione reductase, and increase in osmotic adjustment and starch metabolism [124, 125].

Several methods of seed priming have been developed in order to revive seeds under salt stress conditions. Some of these methods are hydro-priming, osmopriming, solid matrix priming, hormonal-priming, bio-priming, chemical priming, and nutripriming [13]. In recent years, many studies have been reported to exhibit the

positive effects of seed priming on germination under salinity conditions in many crops (**Table 2**).

Hydro-priming is the simplest and one of the mostly used seed priming method. Hydro-priming depends on seed soaking in pure water without chemical substances for 6–24 h and re-drying to original moisture content prior to sowing without emergence of radicle [144]. This method is a low-cost and environmentally friendly due to no use of additional chemicals. The uncontrolled water uptake by seeds is major disadvantage of this technique. Rapid hydration may cause leakage of

Plant	Treatment	Alleviating effect	Reference
Barley (*Hordeum vulgare* cv. Bülbül 89)	Priming with aqueous solution of 30 μM H_2O_2 for 24 h at room temperature	H_2O_2 increased the germination index from 16.71 to 25.07%, and from 8.19 to 14.65% under 250 mM and 300 mM NaCl, respectively	[126]
Tomato (*Solanum lycopersicum* cv. Hezuo 903)	Priming with 100 μM Epigallocatechin-3-Gallate (EGCG) at 28 ± 3°C	EGCG increased germination rate and index from 84.7 to 97.0%, and from 29.4 to 35.2%, respectively	[127]
Wheat (*Triticum aestivum* cv. Chamran)	Priming with 0.5 mM spermidine for 24 h, 25 mM proline for 2 days, or 1.5 mM silicon (K_2SiO_3) for 6 h	Spermidine, proline, and K_2SiO_3 enhanced the germination rate by 32, 18, and 17%, respectively, under salinity stress (20 dS m^{-1})	[128]
Zea mays, *Pisum sativum*, *Lathyrus sativus*	Priming with 0.2 g/L GA3 solution for 12 h at room temperature without light.	GA3 enhanced germination percentage from 16.67, 26.67, and 50 to 60, 73.3, and 86.67% in *Z. mays*, *P. sativum,* and *L. sativus,* respectively, and resulted in 20% reduction in mean germination time under salinity stress (12 dS m^{-1})	[129]
Pakchoi (*Brassica chinensis* L. cv Tiancuiqing)	Priming with sodium nitroprusside (SNP) for 2 h in dark at 25 ± 1°C	Germination potential, germination index, and vitality index were increased by 7.67%, 14.20% and 74.51% after 10 μM SNP pre-treatment under 100 mM NaCl	[130]
Melilotus officinalis	Soaking with 10 mM Ca^{2+}	Ca^{2+} significantly increased the germination percentage and recovery germination percentage under 200 mM NaCl	[131]
Melon (*Cucumis melo*)	Priming with 10–50 μM melatonin for 6 h	Melatonin increase the germination percentage from 50 to 80% under salinity stress (14 dS m^{-1})	[132]
Wheat (*Triticum aestivum* cv. Khirman)	Priming with 50 mg L^{-1} ascorbate, 50 mM proline, 25 μM triacontanol, or 100 μM indole acetic acid for 12 h	Priming treatments significantly enhanced germination index and final germination percentage, and reduced mean germination time under salinity stress (12 dS m^{-1})	[133]
Grain sorghum (*Sorghum bicolor* Moench)	Priming with 100–500 mg L^{-1} nano-iron oxide (n-Fe_2O_3) for 10 h and soaking with 10 mg L^{-1} n-Fe_2O_3 for 3 days	Treatments improved the speed and percent of germination under 150 mM NaCl	[134]

Plant	Treatment	Alleviating effect	Reference
Lentil (*Lens culinaris* cv. Ncir)	Soaking with 0.5 mM salicylic acid or 0.1 mM H_2O_2 at 25°C in the dark	Salicylic acid and H_2O_2 enhanced the germination percentage from 71 to 86 and 87%, respectively	[135]
Limonium bicolor	Priming with 80 μM salicylic acid (SA)	SA significantly increased germination rate, germination potential, and germination index of the seeds under 200 mM NaCl	[136]
Sweet sorghum (*Sorghum bicolor* cv. Chuntian 1)	Priming with 288 μM Gibberellin (GA3) for 32–48 h	GA3 significantly increased the water uptake, resulting with increased cumulative germination percentage and germination index under 100 mM NaCl	[122]
Maize (*Zea mays*)	Priming with 2 mM silicon (K_2SiO_3) for 7 days at 25°C in the dark	Silicon significantly enhanced the germination rate and percentage, as well as vitality index under 90 mM NaCl	[137]
Oat (*Avena sativa* cv. NDO-2)	Priming with 150 ppm gibberellin (GA3) for 24 h	GA3 enhanced the germination percentage from 56.64 to 76.03% under 100 mM NaCl	[138]
Cucumber (*Cucumis sativus* cv. Jinyou 1)	Priming with 0.3 mM silicon (NaSi) for 36 h	Silicon enhanced the germination percentage and index, and seedling vigor index under 200 mM NaCl	[139]
Limonium bicolor	Priming with 200 μM melatonin	Melatonin significantly increased germination rate, potential and index under 200 mM NaCl	[140].
Ceratoides lanata	Priming with 10 mM ethephon, 5 μM fusicoccin or 50 μM kinetin	Fusicoccin, kinetin, and ethephon increased the germination percentage from 10 to 40, 50, and 84%, respectively under 900 mM NaCl	[141]
Leymus chinensis cv. Jisheng 3	Priming with 200 μM gibberellins (GA4 + 7), 200 μM fluridone (FLU), 200 μM cytokinin (CK), 100 μM sodium nitroprusside (SNP), or 100 μM thiourea (TH) in the dark or light	GA and FLU significantly increased the germination percentage from 7 to 23 and 59% in the light, respectively, while SNP, CK and TH increased the germination percentage from 9 to 54, 55, and 30%, respectively, in the dark under 200 mM NaCl	[142]
Salicornia ramosissima	Inoculation with *Bacillus aryabhattai* SP1016-20	Inoculation with *B. aryabhattai* enhanced the final germination percentage and mean daily germination from 21.3 to 46.7%, and from 1.6 to 4.5%, respectively, under 510 mM NaCl	[143]

Table 2.
The functions of seed priming in plant at the germination stage under salinity condition.

essential nutrients out of the seed during germination, resulting in seed damage in some species [145].

Osmo-priming, also known as osmotic conditioning, involves soaking seeds in aerated low water potential solution including sugar, polyethylene glycol (PEG), glycerol, sorbitol, or mannitol with low water potential instead of pure water, followed by air drying before sowing. Due to low water potential of osmotic solutions, water is absorbed slowly by dry seed, which allows gradual seed imbibition [146]. While osmo-priming promotes activation of early phases of germination, inhibiting radicle emergence. Osmo-priming improves seed germination and enhances general crop performance under salt conditions. Water potential of osmotic agent is critical factor since main purpose is to restrict oxidative damage caused by ROS by inhibiting excess water from entering [147]. If inorganic salts such as NaCl, KCl, KNO_3, K_3PO_4, $MgSO_4$, and $CaCl_2$ are used as an osmo-priming agent, the method is generally referred as halopriming.

In hormonal priming, seed imbibition occurs in the presence of plan hormones such as GA3, ethylene, auxins, and salicylic acid, which can gave effect on seed metabolism. Chemical priming is a promising seed priming technique to enhance germination under high salinity stress. Seeds were pre-treated with different chemical solutions used as priming agents. Chemical agents includes a wide range of both natural and synthetic compounds such as antioxidants (ascorbic acid, glutathione, tocopherol, and melatonin), sodium hydrosulfide, polyamines hydrogen peroxide, sodium nitroprusside, urea, selenium, chitosan, fungicide, etc. [13].

Biopriming involves seed imbibition together with particular bacteria or fungi. These microorganisms are able to create endophytic connections with the plant. As other priming method, this treatment increases rate and uniformity of germination under salt conditions, as well as protects seeds against the soil and seed-borne pathogens [147]. The most frequently used biopriming species are *Bacillus* spp., *Enterobacter* spp., *Pseudomonas* spp., and *Trichoderma* spp. [148].

Seed priming efficiency is influence by many factors and strongly depends on treated plant species and chosen priming technique. Physical and chemical factors including osmotica and water potential, priming agent, duration, temperature, presence or absence of light, aeration, and seed condition also influence priming success and determine germination rate and time, seedling vigor, and further plant development [13, 144].

Conflict of interest

No conflict of interest.

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Author details

Cüneyt Uçarlı
Department of Molecular Biology and Genetics, Istanbul University, Istanbul, Turkey

*Address all correspondence to: ucarlicu@istanbul.edu.tr

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