Seed Priming Technology in the Amelioration of Salinity Stress in Plants

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Abstract

A large proportion of the global cultivable land is inflicted by saline conditions. Several popular plants and staple crops cannot be cultivated on these vast stretches of land due to their susceptibility to salt stress. Crops growing under such suboptimal conditions exhibit deteriorated physiological development and compromised yields. Several agro-biotechnology-supported programmes are available to enhance plant salt tolerance. Among them, seed priming or 'pretreatment' is the most acceptable one from the point of biosafety and socio-economic views. Seed priming provides an abiotic stress-like condition to the dormant seed. It partially reprogrammes the seed metabolome so that it experiences such suboptimal condition and can better adapt to salt stress. Partial hydration of the seed during priming weakens the endosperm, channelizes the energy reserves, makes the seed ready for radicle protrusion (germination) and recharges the entire antioxidant machinery. This chapter provides an insight into the multiple mechanisms via which seed priming with various inorganic as well as endogenous agents can ameliorate salinity stress-related damages across multiple plant species.

Keywords

Antioxidative machinery · Protective agents · Seed priming · Salinity stress · Salt tolerance

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5.1 Introduction

Abiotic stresses like salinity, drought, heavy metal toxicity, irradiation, etc. lead to large-scale crop losses throughout the world. Among these environmental challenges, salt stress is most prevalent in arid, semiarid and coastal regions and spreads easily in the irrigated lands (Munns and Tester 2008). The FAO report (2011) highlights that 60–80 million hectares of land are inflicted by salt. This ultimately will lead to the loss of about 50% of the cultivable lands by the twenty-first century. High salt content in the soil or the irrigated water directly interferes with seed germination and seedling growth, thus making most plants susceptible to this kind of abiotic stress (Hubbard et al. 2012). Salt stress delays the advent of germination in susceptible plant seeds (Thiam et al. 2013). An interesting contradiction has been noted in the development of plants in response to low and high salt concentrations (Khan and Weber 2008). It was seen that whereas low salt levels promote seed dormancy, high salt concentrations directly inhibit seed germination. However, both these stress inductions ultimately decrease the germination rate and thus lead to phenotypically retarded development (Khan and Weber 2008). Several crops like *Oryza sativa*, *Zea mays*, *Brassica oleracea*, *Abelmoschus esculentus*, *Vigna unguiculata*, *Apium graveolens*, *Foeniculum vulgare*, *Petroselinum crispum*, *Raphanus sativus*, *Ipomoea aquatica*, *Silybum marianum*, *Lactuca sativa*, *Glycine max*, etc. are reportedly sensitive to a gradient of salt concentrations (Banerjee and Roychoudhury 2016a; Basu and Roychoudhury 2014; Ibrahim 2016).

Esechie (1995) showed that the top 10 cm layer of the soil accumulates higher salt levels than the lower layers. Seeds of cultivated crops are usually sown in this top layer. High evapotranspiration in plants growing in the arid environments results in water loss and accumulation of salt around the roots. This retards translocation and crucial physiological processes (Bernstein and Hayward 1958). Hence, novel strategies are required to ameliorate salt stress in developing crop plants. Transgenic technology has often been adopted to generate genetically modified (GM) plants overexpressing a target gene which confers stress tolerance. However, this technology faces several biosafety issues across multiple countries, and hence such GM plants cannot be popularly marketed. Thus researchers have designed a novel technology called ‘seed priming’ where an inorganic chemical solution or an endogenous osmoprotectant or ‘eliciting factor’ is purified and used as the pretreating agent to make the seeds tolerant to future stress exposures (Tanou et al. 2012). In this technology, the seeds are hydrated in a prescribed solution containing the optimum concentration of the ‘eliciting factor’ and then dried. This improves germination, triggers multiple epigenetic alterations and up-regulates genes encoding stress-responsive transcription factors (TFs) (Farooq et al. 2009; Bruce et al. 2007). The treated seeds reportedly exhibit higher germination and seedling emergence rates under stress conditions in comparison to the non-treated seeds (Sharma et al. 2014). Studies show that seed priming can even improve crop productivity under optimum conditions (Jisha et al. 2013). The popularity of seed priming lies in its easy usage, low cost and lesser environmental risk (Ibrahim 2016).

5.2 Salinity and Seed Germination

Salt stress primarily increases the soil osmotic potential which results in constrained water and solvent uptake via roots (Daszkowska-Golec 2011). The osmotic balance in the plant gets disrupted due to generation of reactive oxygen species (ROS) like hydroxyl radicals, superoxides and hydrogen peroxides (Das and Roychoudhury 2014). Massive oxidative stress caused by Na^+ and Cl^- toxicity jeopardizes macromolecular structures and membrane integrity and even affects embryo development. Physiological processes like photosynthesis, growth, respiration and flowering are severely inhibited by salt stress (Roychoudhury and Chakraborty 2013). The overall systemic deterioration leads to cellular apoptosis coupled with the degeneration of membrane lipids, enzymes and nucleic acids (Banerjee and Roychoudhury 2017a). Peroxidation of membrane lipids produces malondialdehyde (MDA), an important stress marker in plants. Such MDA levels sharply increase in salt-sensitive plants exposed to stress (Das and Roychoudhury 2014).

Salinity-induced ROS accumulation triggers the up-regulation of *osmotic stress responsive* (*OR*) genes and their upstream transcription factors (TFs) in a cultivar-dependent fashion (Roychoudhury et al. 2013; Banerjee and Roychoudhury 2017b). The *OR* gene products confer tolerance in specific cultivars of the crops exposed to salt stress. The salt-tolerant cultivars exhibit higher expression of antioxidant enzymes like superoxide dismutase (SOD), peroxidase (POX), catalase (CAT), glutathione reductase (GR), etc. Most of these enzymes restore the cellular oxidative equilibrium by operating through the ascorbate-glutathione cycle (Anjum et al. 2015). Recent studies have also highlighted the massive histone modifications, DNA methylation and chromatin remodelling occurring in signature genomic regions of the plants exposed to salinity (Banerjee and Roychoudhury 2017c). The transposon-associated differentially methylated regions (DMRs) in IR-64 (stress susceptible), Pokkali (salt tolerant) and Nagina 22 (drought tolerant) rice cultivars were closely related to the transcript abundance of the protein-coding genes (Garg et al. 2015). However, close association of the hypermethylated silenced heterochromatin with the small RNAs (smRNAs) was noted (Banerjee et al. 2016). This clarified the existence of a crosstalk among the chromatin methylation status, gene expression and smRNA abundance during salt stress response in rice.

5.3 Seed Physiology and Priming

Seed hydration triggers germination via three stages: imbibition, lag phase and radicle protrusion through the testa (Ibrahim 2016). Priming promotes partial hydration of seeds. This effectively accelerates pregermination metabolism but is not enough to facilitate the transition of a dormant seed towards complete germination (Paparella et al. 2015). Hence priming converts a metabolically naive seed into a quasi-metabolically active unit. However, such quasi-metabolic state does not support the complete emergence of the radicle.

Table 5.1 The different applied seed priming techniques

Seed priming technique	Nature of the treatment
Hydropriming	Water treated
Osmopriming	Aqueous solution of osmolytes like polyamines, etc.
Halopriming	Inorganic salt solution
Hormone priming	Phytohormones like abscisic acid (ABA), salicylic acid (SA), etc.
Hardening	Hydrated seeds are redried
Solid matrix	Solid materials like ground Leonardite Shale (Agro-Lig), etc. mixed with water in known proportions
Humidification and stratification	Seed processing like cold and moist treatments to promote faster germination after sowing
Physical	Irradiation, heat, etc.

The next crucial phase is the post-priming redrying (or drying back) of the seeds to restore their relative moisture content back to the initial control levels. Redrying of the primed seeds at the correct stage is extremely important for seed storage, preserving seed longevity and tolerance towards abiotic stresses (Ratikanta 2011). It has been reported that the partially hydrated seeds in the imbibition or lag phase tolerate redrying without significant physiological deteriorations (Rajjou et al. 2012). However, seeds with already emerged radicles if redried usually exhibit compromised seed vigour (Rajjou et al. 2012). The rate of redrying also regulates seed viability in due course (Gurusinghe and Bradford 2001). Bruggink et al. (1999) stated that the drying back of the primed seeds should be performed slowly as this improves seed longevity and tolerance to desiccation.

5.4 Seed Priming Techniques

The classification of the priming techniques varies with the chemical nature of the priming agent. Eight different priming techniques are usually reported (Ibrahim 2016). They have been highlighted in Table 5.1. Out of the different priming strategies, hydro-, osmo-, halo- and hormone priming are the most popular (Paparella et al. 2015; Maiti and Pramanik 2013). Depending on the technique to be used, other variable parameters also require standardization to gain optimum ameliorative results. These variables include water potential, priming duration, temperature, seed vigour, cultivar and post-priming storage conditions (Maiti and Pramanik 2013).

5.5 Priming-Induced Alterations Which Ameliorate Salt Stress in Susceptible Plants

Priming promotes embryo swelling and accelerates the development of immature embryos. The partial hydration state reduces the physical resistance of the endosperm, improves physiological parameters and leaches out the chemical inhibitors of germination (Bewley et al. 2013). Sadeghi et al. (2011) reported that priming modifies the seed metabolic balance as a result of which germination and seedling development is more rapid even under suboptimal saline conditions. Such stress tolerance is facilitated by metabolome reprogramming and generation of ‘priming memory’ in seeds (Pastor et al. 2013). ‘Priming memory’ is supposedly epigenetic signatures etched within the seed genome during the stress-like conditions created as a result of seed priming (Banerjee and Roychoudhury 2017c). Such epigenetic alterations in the chromatin architecture lead to the overexpression of several stress-responsive genes like *late embryogenesis abundant* (*LEA*), whose protein products confer tolerance towards salt stress (Banerjee and Roychoudhury 2016a; Roychoudhury et al. 2007).

Sharma et al. (2015) showed accelerated germination in the primed seeds. Such improvements could be attributed to specific germination-associated genes which get up-regulated in the primed seeds (Sharma et al. 2015). Several antioxidant genes also exhibit increased expression as the entire metabolic equilibrium of the seed is altered after optimum priming (Sadeghi et al. 2011). Such antioxidants promote seed germination and seedling development by scavenging the toxic ROS and lowering oxidative stress under saline conditions (Kubala et al. 2015). Salt stress imposes large-scale oxidative stress in the plant. If uncontrolled, this can lead to chromosomal damages, protein degradation and metabolite leakage (Netondo et al. 2004). Oxidative stress-induced membrane peroxidation triggers the accumulation of MDA which inhibits the activities of crucial enzymes (Younesi and Moradi 2015). Priming reportedly reverses these degenerative effects of salt stress and facilitates early replication, transcription and chromosomal repair (Roychoudhury and Chakraborty 2013).

The abiotic stress tolerance generated by seed priming is conferred via the synchronization of several physiological, biochemical, systemic, cellular and molecular modulations (Siri et al. 2013). The metabolome reprogramming enables mobilization of energy reserves via endosperm weakening and promotes the expansion and initial development of the dormant embryo (Chen and Arora 2011). This boosts the germination potential of the seed. The activities of several enzymes which facilitate reserve mobilization are enhanced. These are essentially proteases, lyases and amylases (Varier et al. 2010). Proper seedling development is allowed by inducing cell division, elongation, plasma membrane fluidity and stress-responsive proteins like the heat shock proteins (HSPs) and LEAs. Reports have shown alterations in H^+/ATPase activities and even in the transcriptome and proteome of the primed seeds (Ibrahim 2016). Stress tolerance in the primed seeds is also mediated by an increased potential in protein synthesis and post-translational modifications and by maintaining the optimum quotient for the translational turnover (Kubala et al. 2015).

Bakht et al. (2011) reported that seed priming efficiently eliminated the harmful Na^+ and Cl^- ions via activating membrane efflux pumps. On the contrary, the active uptake of inorganic ions facilitates the accumulation of K^+ and Ca^{2+} ions which in turn lowers the cellular osmopotential and promotes water uptake under saline conditions. Apart from these beneficial effects, K^+ ions balance membrane potential and turgor, whereas Ca^{2+} ions maintain the cellular morphology and integrity and mask the growth inhibitory effects of Na^+ ions (Summart et al. 2010; Gobinathan et al. 2009).

A large number of inorganic and organic solutes have been isolated from plants which mediate osmotic adjustments and confer salt tolerance. Solutes like proline (Pro), glycine betaine, free amino acids, soluble sugars, etc. undergo accumulation in the seeds and seedlings after osmopriming. These solutes might also be used as the priming agents to ameliorate salt susceptibility in plants (Roychoudhury and Chakraborty 2013). A chronological representation of the significant priming reagents used across several plant species to generate salt tolerance is presented in Table 5.2. Antioxidant enzymes like SOD, CAT and peroxidase (POX) also exhibit increased ROS scavenging upon seed priming (Nawaz et al. 2012). Compatible solutes like polyamines [putrescine (Put^{2+}), spermidine (Spd^{3+}) and spermine (Spm^{4+})] maintain cellular osmolarity and membrane integrity by chelating out the toxic Na^+ ions (Paul and Roychoudhury 2016; Roychoudhury et al. 2008). Similar antioxidative effects are conferred by seed priming using ascorbic acid and glutathione (Roychoudhury et al. 2012). Imbibition with the universal stress hormone, abscisic acid (ABA), generates a ‘stress memory’ in the seeds and makes them salt tolerant (Roychoudhury et al. 2009). Priming also induces the accumulation of photoprotective pigments like anthocyanin which exhibit ROS scavenging and plant protection (Banerjee and Roychoudhury 2016b). Overall, the priming strategies utilized to generate salt tolerance reduce MDA content and optimize ROS levels via accumulation of multivariant antioxidants and protective proteins (Nawaz et al. 2012).

5.6 Conclusion and Future Perspectives

Priming is a biologically safe and cheap crop expansion technology which modifies the seed metabolome and makes the tissue ready to tolerate suboptimal conditions like salinity. From the mechanism of stress amelioration by several priming agents (Table 5.2), it can be summarized that they recharge the antioxidant machinery and up-regulate multiple stress-responsive genes (Paul and Roychoudhury 2017). This promotes seed development and germination even under adversely saline conditions. Seed priming is also economically cheap since a small volume of priming solution is sufficient for seed imbibition, and this solution can even be reused. In spite of the huge potential of this technology, little information regarding its molecular mechanisms actually exists. One such perspective is the epigenomic basis of ‘stress memory’, which is required to be unravelled. Precise concentrations of the priming agents are extremely important for agronomic purposes as unusually high concentrations can cause irreversible damages to the developing seeds. Thus, future investigations revolving around the molecular and metabolomic platforms in this field shall bear credible impacts.

Table 5.2 Some seed priming approaches adopted to ameliorate salinity stress across susceptible plant species

Type	Agent	Concentration/dose	Treatment time	Plant Species	Salt tolerance	Mechanism	References
Halopriming	KNO_3	0.25 mM	–	*Silybum marianum*	^	Improved germination indices and peroxidase activity	Zavariyan et al. (2015)
	Silicon priming (Na_2SiO_3)	30 mM	–	*Triticum aestivum*	^	Accumulation of Ca^{2+} and K^+ ions	Azeem et al. (2015)
	KCl	10 mM	36 h	*Capsicum annuum*	^	Increased proline accumulation	Aloui et al. (2014)
	$CaCl_2$	2 mM	24 h	*Cucumis sativus*	^	Increased proline accumulation	Joshi et al. (2013)
	NaCl	300 mM	24 h	*Solanum lycopersicum*	^	Increased gibberellin content promoting endosperm weakening and germination	Nakaune et al. (2012)
	NaCl	100 mM	36 h	*Cucumis melo*	^	Increased proline, soluble carbohydrates and antioxidants	Farhoudi et al. (2011)
	KNO_3	−1.0 MPa	24 h	*Helianthus annuus*	^	Better osmoregulation	Bajehbaj (2010)
	NaCl	1 mM	–	*Capsicum annuum*	^	Generated ‘stress memory’	Khan et al. (2009)
	KCl, KNO_3, $CaCl_2.2H_2O$, $Ca(NO_3)_2.4H_2O$	Varying concentration	12 h	*Triticum aestivum*	No change	–	Ashraf and Iram (2002)
	Mixed salt	–	–	*Oryza sativa*	^	Increased activities of amylases, root dehydrogenase and shoot catalase	Chang-Zheng et al. (2002)
	$CaCl_2$	10–60 mmol L^{-1}	12 h	*Gossypium hirsutum*	˅	Species-specific effect; low germination	Xiao-Fang et al. (2000)
	KNO_3 $CaCl_2$	–	–	*Cajanus cajan*	^	Accumulation of proteins, free amino acids and soluble sugars	Jyotsna and Srivastava (1998)

(continued)

Table 5.2 (continued)

Type	Agent	Concentration/dose	Treatment time	Plant Species	Salt tolerance	Mechanism	References
Osmopriming	Spermidine	5 mM	8 h	*Oryza sativa*	^	Up-regulation of several stress-responsive genes and transcription factors; enhanced expression of membrane Na^+ efflux pumps	Paul et al. (2017)
	Glycine betaine	10 mM	24 h	*Capsicum annuum*	^	Decreased MDA levels due to higher accumulation of proline	Roychoudhury and Banerjee (2016) and Korkmaz and Şirikçi (2011)
	Nitric oxide	75 µM (Na-nitroprusside)	24 h	*Jatropha curcas*	^	Increased accumulation of glutathione and ascorbate in the endosperm-embryo axis; higher activities of catalase 1, catalase 2 and glutathione reductases (GR1 and GR2)	Gadelha et al. (2017)
	H_2O_2	–	–	*Cakile maritima, Eutrema salsugineum*	^	Redox balance was restored	Ellouzi et al. (2017)
	Spermine	2.5 mM	8 h	*Oryza sativa*	^	Osmo-protection	Paul and Roy choudhury (2016)
	β-amino butyric acid	1 mM	6 h	*Vigna radiata*	^	Increased accumulation of proline, total carbohydrates, total protein; enhanced activities of nitrate reductase, superoxide dismutase and guaiacol peroxidase	Jisha and Puthur (2016)
	Trehalose	10 mM	48 h	*Oryza sativa*	^	Enhanced the activities of multiple antioxidant enzymes	Mostofa et al. (2015)
	Ascorbic acid	Variable	–	*Triticum durum*	^	Proteins associated with metabolism, energy, disease, defence and storage showed increased abundance	Fercha et al. (2014)
	Ascorbic acid	0.5 mM	24 h	*Cucurbita pepo*	^	Increased activities of catalase and peroxidase	Fazlali et al. (2013)
	Choline	5 mM	24 h	*Triticum aestivum*	^	Increased glycine betaine accumulation and maintenance of osmotic potential	Salama et al. (2011)

Physical priming	UV-C	0.85 KJ m^{-2}	1–4 min	*Lactuca sativa*	^	Increased levels of phenolics and flavonoids which efficiently scavenged the diphenyl-picrylhydrazyl radicals	Ouhibi et al. (2014)
Hormone priming	Salicylic acid (SA) + fish flour	0.1 mM SA	Overnight	*Triticum durum*	^	Enhanced activities of phenylalanine ammonia lyase, peroxidase; accumulation of phenolics and flavonoids	Karadag and Yucel (2017)
	Methyl jasmonate	25 μmol L^{-1}	–	*Brassica oleracea*	^	The contents of indolic glucosinolates, glucobrassicin, neo-glucobrassicin, anthocyanins and chlorogenic acid derivatives increased	Hassini et al. (2017)
	Salicylic acid	0.5 mM	Overnight shaking at 150 rpm	*Triticum durum*	^	Accumulation of total phenols, flavonoids and carotenoids; increased activities of phenylalanine ammonia lyase and ascorbic acid oxidase	Yucel and Heybet (2016)
	Melatonin	–	–	*Vicia faba*	^	Increased photosynthetic efficiency, total carbohydrates, total phenols, indole acetic acid, K^+ and Ca^{2+} levels	Dawood and El-Awadi (2015)
	ABA	30 ppm	8 h	*Phaseolus vulgaris*	^	Increased phosphatidylcholine/ phosphatidylethanolamine ratio and confers root cell membrane protection	Salama et al. (2015)
	Melatonin	1 μM	24 h	*Cucumis sativus*	^	ABA catabolism and gibberellic acid biosynthesis were promoted; the antioxidant machinery recharged	Zhang et al. (2014)
	Gibberellic acid (GA_3)	4.5 mM	12 h	*Lactuca sativa*	^	ABA biosynthesis is suppressed which triggers efficient germination	Hela et al. (2012)
	Gibberellic acid (GA_3)	20 mg L^{-1}	24 h	*Foeniculum vulgare*	^	ABA biosynthesis is suppressed which triggers efficient germination	Sedghi et al. (2010)

^ Enhanced
˅ Decreased

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