Seed Priming-Mediated Improvement of Plant Morphophysiology Under Salt Stress

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Abstract This chapter is describing the adverse effect of the salinity stress on the crop growth and development and how seed priming can alleviate salinity-induced devastating effects on plants. Growth of plant under salt stress is affected negatively due to oversynthesis of reactive oxygen species (ROS), leading to oxidative damage to biomolecule and plant membranes. The water stress and accumulation of toxic ions are the other major effects observed under salt stress. Overproduction of ROS reacts with key cellular molecules and metabolites including proteins, lipids, photosynthetic pigments, and DNA. However, numerous plant species have effective

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defense system based on antioxidants that activates once plant undergoes any abiotic stress. Among various antioxidants, nonenzymatic and enzymatic are essential to detoxify ROS and its scavenging. Recently, seed priming has gained popularity as it develops tolerance in plants against salinity during the germination process and seedling development stage. In various types of environmental stresses, the different priming techniques as osmopriming, hydropriming, hormonal priming, nutrient priming, chemical priming, bio-priming, matrix priming, and redox priming are employed. There has been increasing evidence that priming stimulates the cellular defense response that induces tolerance to biotic and abiotic stresses upon exposure in the field.

Keywords Seed priming · Salt stress · Reactive oxygen species · Antioxidants · Abiotic stress tolerance

1 Introduction

Among various abiotic stresses, salt stress is considered as a major threat to agricultural crops globally. Crop plant experiencing salinity shows poor growth due to toxic ion accumulation and disturbed water relation balance (Rehman et al. 2016). The enhanced accumulation of reactive oxygen species including hydrogen peroxide (H_2O_2), singlet oxygen ($^1O_2$), and superoxide anions ($O_2^{\bullet-}$) under salt stress induces oxidative damage to plants (Ashraf 2009; Ali et al. 2017). These species are highly reactive and promptly react with biomolecule substances and essential cellular metabolites such as DNA, proteins, pigments, and lipids (Ashraf 2009). Accumulation of ROS leads to multiple impairments such as deactivation of antioxidative defense system and lipid peroxidation (Tanou et al. 2009; Anjum et al. 2015, 2016a; Shahzad et al. 2018 a, b; Fahad et al. 2019), although H_2O_2 production under stressful environment causes oxidative damage. However, this molecule functions as a signaling molecule in a variety of biological processes including activation of antioxidant enzymatic system that helps plant to adjust under stress environment (Qiao and Fan 2008; Tanou et al. 2009; Hernandez et al. 2010; Tanveer and Shabala 2018).

Accumulation of ROS, e.g., malondialdehyde, that appears to be mutagenic product of lipid peroxidation resulting in cell damage and effectively used as marker for cell membrane injury (Riahi and Ehsanpour 2013; Anjum et al. 2016a, b). Conversely, Li et al. (2010) reported that malondialdehyde production depends on stress type, cultivar/crop type, and strength of antioxidative defense mechanism. Effective antioxidative plant defense system including accumulation of enzymatic [catalase (CAT), glutathione reductase (GR), ascorbate peroxidase (APX)] and nonenzymatic (phenolics, proline, flavonoids, tocopherol, ascorbic acid) antioxidants helps in ROS detoxification (Ali and Ashraf 2011; Anjum et al. 2017).

Ascorbic acid (AsA) and phenolics are important physiological nonenzymatic antioxidant (Rice-Evans et al. 1996); AsA has a powerful role to complete and strengthen the antioxidation and plant defense process. Moreover, proline concentration in leaf, AsA, tocopherol, and glutathione significantly contribute to ROS scavenging and are able to maintain cell water potential, i.e., osmotic adjustment (Kishor et al. 2014). Contrarily, a study by Signorelli et al. (2016) reported that proline has no significant ability to scavenge ROS (NO2, $O_2^{\bullet-}$, NO, peroxynitrite) due to its selective antioxidant potential to convert OH as a second defense line. Generally, it has been observed that proline accumulates in plants under salt stress; but salt-sensitive plant accumulates less proline than salt tolerant (Habib et al. 2012; Anjum et al. 2015).

Under stress conditions, cultivars having high yield potential seem to be more stress sensitive leading to their poor growth and performance. To achieve high yield potential, stress tolerance imparts in cultivars following various non-breeding and breeding approaches with particular focus on imperative physiological and biochemical traits. Furthermore, exogenous application of different chemicals (with required nutrient) using different methods is also an attractive option to enhance stress tolerance (Anwar et al. 2012) in crops. Among various methods, seed priming with nutrients is considered as handsome and effective approach (Ibrahim 2016; Rehman et al. 2018).

In many crops, germination and seedling emergence are more sensitive to adverse growing conditions and significantly contribute in uniform crop stand (Ali et al. 2017), resulting in higher yield. Similarly, salt stress negatively affects the germination by disturbing physio-biochemical processes including ionic imbalance, oxidative stress, and osmotic stress. Various studies show that salt stress slows down the germination of seed by reducing water imbibition, disruption of proteins structure, and stored food mobilization (Ibrahim 2016; Shahzad et al. 2019). Conversely, priming of seed helps in early seed germination by accelerating the pre-germination metabolic process (Paparella et al. 2015).

Seed priming stimulates the germination and improves seedling development predominantly through decreasing the time period of lag phase, DNA repair during water imbibition, activation of enzymes and germination metabolites, and osmotic adjustment (Lee and Kim 2000; Farooq et al. 2006; Brocklehurst and Dearman 2008; Hussian et al. 2015). Seed priming includes different methods such as hydropriming, osmopriming, chemical priming, nutrient priming, hormonal priming, and redox priming which are considered promising techniques for various crops and can be adopted under wide stressful environments (Jisha et al. 2013; Paparella et al. 2015). Various reports have confirmed the beneficial impact of seed priming under stress conditions that includes cellular defense response activation that helps crop plant to tolerate under abiotic and biotic stress under field conditions (jisha et al. 2013).

2 Priming and Salt Stress Tolerance

2.1 *Plant Morphology*

In salinity stress, the germination is substantially reduced or delayed because of ion toxicity (Na^+, Cl^-) and obstructed water uptake that induce osmotic stress (Hasegawa et al. 2000; Khaje-Hosseini et al. 2003; Farsiani and Ghobadi 2009). However, under salinity stress, seed priming seems to be an effective technique that helps to remove problem of poor germination. For instance, germination rate and seedling vigor index of salt-stressed maize crop substantially improved with hydropriming (Janmohammadi et al. 2008). A research study conducted by Ashraf and Rauf (2001) found that under salt stress, water soaking of maize seed showed uniform and vigorous germination.

Different seed priming methods have been evolved and widely practiced in various field crops including wheat, chickpea, and cotton (Iqbal and Ashraf 2007; Kaur et al. 2002; Casenave and Toselli 2007a; Ullah et al. 2019) to enhance the uniformity of germination, seedling vigor, and acceleration of vegetative growth resulting in higher grain yield (Farooq et al. 2018a, b, c). Under suboptimal conditions, primed seed showed early germination, healthy seedling, and overall better growth than non-primed seeds (Khalil et al. 2001; Sivritepe et al. 2003). Earlier, several reports are available that support the positive impact of seed priming on the germination, growth, and tolerance against stressful environment in various crops such as maize, wheat, lentil, sugarcane, and cucumber (Foti et al. 2008; Ghiyasi et al. 2008; Ghassemi-Golezani et al. 2008; Patade et al. 2009; Ghassemi-Golezani and Esmaeilpour 2008).

Under salinity stress, higher amount of salt accumulated in spaces between the cells that cause imbalance in water relations (Zhang et al. 2006). Seed priming has also been adopted in numerous field and horticultural crops, to decrease the emergence/germination time, to ensure uniform stand establishment (Farooq et al. 2005; Ashraf and Foolad 2005), and to improve the allometric traits.

Uniform germination, growth, and vigorous crop stand are not achieved in late-planted wheat causing low yield under rice-wheat rotation; thereby, sowing of primed wheat seed helps in early germination with uniform crop stand, ultimately leading to better grain yield (Kant et al. 2006). Lee et al. 1998; Kant et al. 2006 stated that uniform crop stand in response to seed priming occurs due to stimulation in germination metabolism, which accelerates germination rate with uniform seedling. Seed priming ensures the timely breakdown of food reserve through activating germination metabolism which helps seed to make up germination process within less time (Kant et al. 2006; Farooq et al. 2007, 2017).

In addition, sowing of primed seed produced highest tillers in terms of number and fertility. In a comparison of osmopriming and hydropriming, it was found that hydropriming shortens the emergence period and improved the vigor and dry weight of seedling (Ahmadi et al. 2007). Harris (2006) also found that seed priming in wheat (for <12 h) proves to be more beneficial than other techniques as it positively improves germination, decreases emergence time, and has early flowering and maturity phase, resulting in higher grain yield.

Priming of various canola cultivars with different solutions (KCl 2%, KCl 0.5%, KH_2PO_4 0.01%) showed positive relation with germination, stem growth, and root dry biomass and also strengthens plant defense to cope stressful environment (Saeidi et al. 2008).

2.2 Plant Physiology

Seed imbibition and lag phase are completed during the process of priming, and when these primed seeds are sown, these two phases of water absorption of seed are shortened (Khan et al. 2009). Improved germination of primed seed attributed to inside swelling of seed embryo (Elouaer and Hannachi 2012) that mediates in water uptake. Activation of pre-germination metabolism except radicle protrusion occurs during the process of seed priming (Farooq et al. 2007). During the process of imbibition, certain steps including, decrease in resistance of endosperm, membrane and DNA repairing, embryos become mature and the germination inhibitors are leached (Bewley et al. 2013). Hence, under adverse environments, the seedlings grow/emerge at a faster and vigorous rate and perform better than the non-primed seeds (Sadeghi et al. 2011).

Induction of tolerance against stress conditions in primed germinated seeds may be attributed to manifestation of cross tolerance mechanism which consists of two approaches (Chen and Arora 2013). The first strategy is the activation of germination metabolism such as mobilization of reserve materials, endosperm weakening, embryo expansion, and enhanced energy metabolism (Li et al. 2010; Sun et al. 2010) which cause quiescent dry seed transition into a germinating phase with high germination vigor. The second approach reflects the imposition of abiotic stress environment on seed which inhibits emergence of radicle but accelerates cross tolerance in response to stress. The combination of these approaches establishes “priming memory” within the seed that reactivates later, upon exposure to stress which builds up strong tolerance in germinated seeds (Bruce et al. 2007; Pastor et al. 2013).

The process of osmoregulation in plant starts upon the active uptake of inorganic ions. Alleviation of negative impact of salt stress on seed germination and health seedling development can be achieved by seed priming that increases the accumulation of Ca^{+2} and K^+ and reduces accumulation of Cl^- and Na^+ in developing seedling (Iqbal et al. 2006; Afzal et al. 2008; Bakht et al. 2011), resulting in more water uptake with low osmotic potential (Ashraf 2009). Potassium is essential for activation of enzymes, for turgor and membrane potential balance, and in osmotic regulation in cells (Cherel 2004). Like potassium, calcium (Ca) also plays very important roles in cell elongation and division, maintains cell wall integrity, regulates the uptake of nutrients across the membrane, and improves uptake of water in plants and alleviates the adverse effect of Na^+ during plant growth (Patade et al. 2009; Gobinathan et al. 2009; Summart et al. 2010).

2.3 Leaf Gas Exchange

Seed priming with saponin improves the tolerance against salinity in quinoa by stabilizing the stomatal conductance and leaf photosynthetic rate resulting in better gas relations (Yang et al. 2018). Under salinity, abscisic acid (ABA) concentration increases in leaf (Amjad et al. 2014) which may inhibit some CO_2 diffusion rate due to increased stomatal closure induced by higher ABA concentration resulting in disrupted stomatal conductance (Liu et al. 2005, 2006). Contrarily, priming with saponin decreases the ABA concentration and improves gas relations, i.e., stomatal conductance (Yang et al. 2018). Another study showed that seed priming with triacontanol improves leaf gas exchange (Sarwar et al. 2017) due to its substantial role in stomatal regulation by upregulating the photosynthetic genes and increases CO_2 rate under salt stress (Chen et al. 2002; Perveen et al. 2010). Seed priming with auxin enhances the gas relations in salt-tolerant and non-salt-tolerant cultivars that is attributed to the tryptophan-dependent indole acetic acid involving in the opening of stomata (Merritt et al. 2001) and enhances CO_2 assimilation rate under salinity (Iqbal and Ashraf 2013).

2.4 Transpiration

Seed priming with tryptophan increased the rate of transpiration in both salt-sensitive and salt-tolerant wheat cultivars (Iqbal and Ashraf 2013). Brassinolide priming in maize improved the transpiration rate by 11% under drought stress (Anjum et al. 2011). This could be due to the improvement in leaf water balance by brassinolide application (Sairam 1994). Various studies in literature show extensive work on brassinosteroid application in improving abiotic stress tolerance in plants (Shahzad et al. 2018a; Sharma et al. 2018; Tanveer et al. 2018a, b). Priming of barley seeds with $CaCl_2$ improved drought tolerance attributed to enhanced transpiration rate without negative effects on the leaf turgor status and better stomatal aperture (Kaczmarek et al. 2017). Priming of *Brassica juncea* (Fariduddin et al. 2003) and safflower (Mohammadi et al. 2017) with salicylic acid helped to improve the stomatal conductance, better water status, and mesophyll conductance resulting in higher transpiration rate. A positive correlation has been established between transpiration and stomatal conductance, with increase in stomata opening rise in transpiration observed. Seed priming helps in vigorous plant growth with well-established root system; thus, enhancement of transpiration rate directly links with better plant water status that may be due to more water uptake by deeper roots (Mohammadi et al. 2011; Abdolahi and Shekari 2013).

2.5 Photosynthesis

In mung bean, priming of β-amino butyric acid aided in alleviating several abiotic stresses, i.e., salinity, high temperature, and drought (Jakab et al. 2001; Cohen 2001; Zimmerli et al. 2008) by enhancing mitochondrial activities, photosynthetic pigments, photosynthesis, and chlorophyll *a* contents resulting in better photosynthesis process (Jisha and Puthur 2016). Moreover, β-amino butyric acid priming substantially stimulated the activities of photosystems I and II and increased the transport, absorption, and trapping of electron per photosystem II (Jisha and Puthur 2016). In rice seeds, priming with PEG (Li and Zhang 2012) and polyamine priming in cucumber (Zhang et al. 2009) enhanced the photosynthetic efficiency by increasing the photochemical efficiency of photosystem II. Seed priming helps to increase mitochondrial number and improve the outer membrane integrity of mitochondria (Benamar et al. 2003; Varier et al. 2010). In maize, seed priming with silicon enhanced the photosynthetic efficiency by improving the chlorophyll contents under alkaline stress (Abdel Latef and Tran 2016) that helped plant to stay green for longer time and tolerate under stressful environment. Another study reported that soybean primed seeds with $CaCl_2$, $ZnSO_4$, and gibberellic acid improved the photosynthesis attributed to higher photosynthetic pigments and better integrity of chloroplast, mitochondria, and membranes (Dai et al. 2017). In safflower, salicylic acid application through seed priming enhanced the photosynthetic rate and chlorophyll content index and the number of chlorophyll pigments such as photoreceptor antennas that also has direct positive effect on the photosynthetic device such as improvement in electron transport chain and stimulates the activities of enzymes involving in the photosynthesis, e.g., rubisco (Mohammadi et al. 2017). Furthermore, salicylic acid prevented the degradation of chloroplast and improved the electron transport capacity by photosystem II resulting in stimulation of net photosynthetic rate and overall photosynthesis process (Shakirova et al. 2003; Fariduddin et al. 2003; Khodary 2004) as observed in soybean, corn, and barley.

2.6 Antioxidant Activities

Seed priming with comprehensive agents aids plant to tolerate against abiotic stresses by improving the activities of antioxidant enzymes by detoxifying the ROS (reactive oxygen species) (Dai et al. 2017). Improvement in antioxidant capacity improves the potential of plant to mitigate damage induced by ROS. Catalase (CAT) and superoxide dismutase (SOD) are considered as the most effective antioxidant enzymes that provide first-line defense against toxic ROS level (Gill and Tuteja 2010). Catalases with maximum turnover have the ability to convert about six million hydrogen peroxide (H_2O_2) molecules to oxygen (O_2) and water (H_2O) per minute only using one molecule of catalases (Gill and Tuteja 2010). Seed priming with $CaCl_2$ and $ZnSO_4$ enhances antioxidant enzyme activities including CAT and SOD and reduces the malondialdehyde contents and lipid peroxidation (Dai et al. 2017). Priming of seed with silicon plays pivotal role in enhancing the tolerance against alkaline stress by accumulating the osmoprotectants and activating the antioxidant machinery (Abdel Latif and Tran 2016) such as SOD, CAT, and peroxidases leading to oxidative stress mitigation. Moreover, silicon application through seed priming improves the contents of antioxidant phenols under alkaline stress (Abdel Latif and Tran 2016). Another study indicated that β-amino butyric acid alleviated the oxidative stress and lipid peroxidation by reducing the malondialdehyde contents and enhancing the proline contents and activities of SOD and guaiacol peroxidase, chitinase, nitrate reductase, and polyphenol oxidase (Jisha and Puthur 2016) under drought and saline stress. Ascorbic acid and salicylic acid priming stimulate antioxidant enzyme activities such as ascorbic acid, ascorbate peroxidases, POD, and CAT and accumulate the osmoprotectants that help to maintain the plant water status under abiotic stress, e.g., salt stress (Carvalho et al. 2011; Ahmad et al. 2012), and protect plant from oxidative stress. In a study, Carvalho et al. (2011) showed that hormonal priming (methyl jasmonate, salicylic acid, and chloroethylphosphonic acid (CEA)) protected maize seedlings from salt stress damage by activating the antioxidant machinery such as glutathione reductase, ascorbate peroxidase, SOD, POD, and CAT.

3 Summary and Future Research Perspectives

Seed priming is an important technique to attain desirable results against several abiotic stresses including salt stress. During the last few years, it has been emerged as a promising approach in inducing stress tolerance due to its involvement in improving overall plant defense against these abiotic stresses. Moreover, it provides a realistic, effective, and smart choice for successful plant protection. Although exact mechanism behind crop improvement is still unknown, however, it has been suggested that seed priming normally helps to regulate plant signaling through activating certain cell signaling pathways and cellular responses. It is therefore needed to further explore the molecular mechanism involving these signaling pathways.

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