Mechanisms of Seed Priming Involved in Salt Stress Amelioration

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M. Hasanuzzaman, V. Fotopoulos (eds.), *Priming and Pretreatment of Seeds and Seedlings*, https://doi.org/10.1007/978-981-13-8625-1_11

Abstract Reduction of photosynthetic rates in plants under salt pressure is triggered primarily by reducing water potential and/or elevated levels of Na^+ and/or Cl^- accumulated in chloroplasts and chlorophyll that are essential for plant health. Much work has been done to create strategies to deal with salinity stress. The use of organic and inorganic compounds, nutrients, and seed priming is among the promising strategies adopted to alleviate the unfavorable consequences of salinity and improve plant yields and yield quality. Seed priming is a commercially used method to improve the germination and vigor of seeds. The purpose of this work is to review the recent literature on plant response to seed priming under salinity stress. A schematic diagram describing the chain reaction following the seed priming was proposed. The diagram illustrates the possible impact of the seed priming on different physiological processes, enhancing tolerance level and final yield. Several mechanisms have been proposed to explain how plants build up many physiological and biochemical adaptations to regulate themselves when using seed priming under saline conditions. The variation on photosynthetic pigment (chlorophyll a, chlorophyll b, carotenoids), photosystem II, and net CO_2 photosynthetic rate; ionic balance; K^+:Na^+ ratio difference; osmolyte accumulation, i.e., proline, glycine betaine, amino acids, and sugars; accumulation of enzymatic like superoxide dismutase, catalase, ascorbate peroxidase, peroxidase, and nonenzymatic antioxidants (i.e., total phenols, flavonoids, ascorbic acid, total carotenoids); membrane stability; and levels of H_2O_2 and malondialdehyde (MDA) contents are among the most important physiological and biochemical plant reaction mechanisms for seed priming that allow plants to cope under saline conditions.

Keywords Antioxidants · Enzymes · Growth · Ionic balance · Osmolytes · Oxidative stress · Photosynthesis · Photosynthetic pigment · Salinity · Salt · Seed priming

1 Introduction

Salinity is one of the most common environmental problems that limits the productivity of plants, particularly in arid and semiarid areas (Ashraf and Harris 2004). Based on the Food and Agriculture Organization (FAO) Soils portal (http://www.fao.org/soils-portal/soil-management/), soil is considered to be saline soil when electrical conductivity (EC) is >0.7 dS m^{-1}. Nevertheless salt-affected soils are characterized by a specific electrical conductivity (EC) of extracts of saturated soil-paste above 4 dS m^{-1} (temp at 25 °C) according to the *USDA Agriculture Handbook*

(1954). More recently, Bresler et al. (1982) stated that soils are rated salt affected beginning at an EC level of 2 dS m^{-1}, as some vegetable, fruit, and ornamental crops undergo from salinity within the EC of 2–4 dS m^{-1}.

Salt-affected soil refers to soils where, with normal plant growth, salts interfere. Depending on salt quantity, salt type, sodium present, and soil alkalinity, salt-affected soils can be divided into saline, saline-sodic, and sodic. There will be different characteristics for each type of salt-affected soil, which will also determine how it can be managed. Based on the FAO Soils portal using the world's FAO/UNESCO soil map (1970–1980), the FAO estimated the total global saline soil area was 397 million hectares and the total sodic soils 434 million ha. However, Nelson and Mareida (2001) estimated approx. 12 million ha of irrigated land may possibly have disappeared from production accordingly of salinization.

Salinity results in many unfavorable effects on the growth of plants due to low osmotic soil potential (osmotic stress), ion effects (salt stress), element imbalances, or a combination of these causes (Ashraf 2004). All these factors cause physiological and biochemical unfavorable effects on plant growth and development (Munns and James 2003). To evaluate plant tolerance to salinity stress, the plant's growth or survival is measured as it integrates many physiological mechanisms that occur within the plant. For plants growing in the saline medium, osmotic balance is essential.

The main strategies for the use of salt-affected soils are use of reclaiming and protective measures to make salt-affected soils suitable for agriculture and utilize salt-affected soils by growing halophytes or salt-tolerant crops/cultivars. The latter approach has been called the "biological approach" (Ashraf 1994) and has significant potential to mitigate the worldwide soil salinity problem. This chapter discuss biological strategies that can increase crop salinity tolerance. Strategies employed to relieve the impacts of salt stress in plants include applying chemical, biological, and physical treatments to seeds, seedlings, or plants prior to exposure to salinity stress. These treatments, mostly used before seed sowing, are anticipated to activate physiological and molecular pathways that allow the seed to react more quickly and/or more strongly after exposure to an environmental stress factor.

Seed priming is a knowledgeable, rational, and low-cost method for fast emergence, increased seedling strength, and improved plant yields under adverse environments (Jisha et al. 2013; Paparella et al. 2015). It is a restricted hydration method that activates metabolic processes before radicular protrusion at the early stage of germination (Hussain et al. 2015).

Under various environmental stresses, different methods of seed priming were utilized that include hydropriming, osmopriming, Chemopriming, nutrient priming, and hormonal priming (Jisha et al. 2013; Paparella et al. 2015). Seed priming promotes germination throughout the process by soaking seeds in solutions with exogenous molecules, i.e., salicylic acid (SA) and acetylsalicylic acid (ASA) (Khan et al. 2009a, b), or metals (Mirshekari et al. 2012), or hormones (Nakaune et al. 2012). Seed priming was proposed to trigger a sequence of physiological developments which increase plant performance grown in salt stress, including the introduction of antioxidant systems (Varier et al. 2010; Eisvand et al. 2010).

The purpose of this chapter is to present a wide overview of plant response under salt stress and the primary treatments in specific organic and inorganic substances and seed priming utilized to seeds/plants with a critical debate of the key accomplishments outlined in this area.

2 Plant Response to Salt Stress

A soil is considered saline once the soil solution's electrical conductivity (EC) is approximately 4 dS m^{-1} (corresponding to 40 mM NaCl), creating an osmotic pressure of approximately 0.2 MPa, which reduces most crop yields (Munns and Tester 2008). Salt stress induces ion toxicity, osmotic stress, nutrient deficiency, and oxidative stress on crops, thus restricting the absorption of soil water and eventually decreasing yield output (Awad et al. 2012; Hellal et al. 2012; Abdelhamid et al. 2013b; Rady et al. 2015, 2016b). Figure 1 shows response of soybean crop grown in soils with three salinity intensities, i.e., 1.12, 6.25, and 9.38 dS m^{-1}, at Fayoum Governorate, Egypt.

Plant species vary for salt tolerance (Blaylock 1994; Bargaz et al. 2016). Salt-tolerant crops (plants less affected by salinity) can adjust the osmotic impacts of elevated levels of salt internally as compared to salt-sensitive crops. Also, salt-tolerant crops can absorb salt soil water more easily. On the other side, salt-sensitive crops have restricted ability for adjustment and are injured at comparatively small levels of salt. In reaction, in sensitive crop cultivars, reductions in yields caused by salinity look more widespread than in tolerant crop cultivars. Several authors report such a reduction in salinity yield (Blaylock 1994; Abdelhamid et al. 2013a; Dawood et al. 2016).

Global studies have shown that salinity affects germination and growth of seedlings in different crops, such as Bagayoko (2012). The effect of salt stress on plant

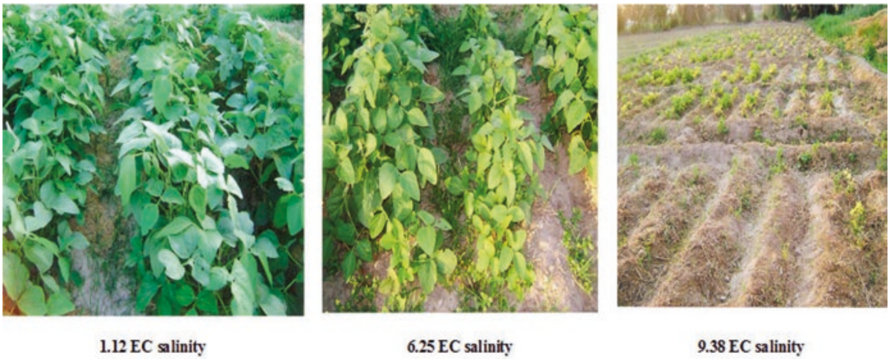

Fig. 1 Soybean crop grown in soils with different salinity levels at Fayoum Governorate, Egypt

can be attributed to the adverse effects of salinity on the cell cycle and differentiation. A general reduction in plant biomass was observed in all plant tissues under salt stress, but it is particularly noticeable in the aerial part (Abdelhamid et al. 2010). Different authors have associated a decrease in plant biomass with a decrease in leaf numbers or leaf abscissions (Dawood et al. 2014b) or a decrease in net assimilation rate and relative growth rate (Rady et al. 2015).

Salinity has several unfavorable effects on plant growth owing to low soil osmotic stress, ionic imbalances, or combined effects of these factors (Ashraf 2004). All these variables affect plant growth and development with adverse physiological and biochemical impacts (Munns and James 2003). The plant's development or survival is evaluated by integrating many physiological processes that happen within the plant to assess the salinity stress tolerance of the plant.

The stress of salinity in the soil significantly reduces nutrient concentrations such as N, K, Ca, and Mg (Sadak et al. 2015; Talaat et al. 2015; Rady et al. 2016b). In addition, salinity reduces plant P uptake owing to precipitation of phosphate ions with Ca ions (Bano and Fatima 2009; Abdelhamid et al. 2010; Bargaz et al. 2016). Some elements have particular toxic effects on plants, such as sodium, chlorine, and boron. Excessive accumulation of Na^+ in cell walls can rapidly trigger osmotic stress and cell death (Munns 2002). Furthermore, salinity has damaging impacts on photosynthesis, primarily due to decreased leaf area, chlorophyll content, and stomatal conductance, and to some degree owing to decreased effectiveness of photosystem II (Netondo et al. 2004).

There is no doubt that there has been noteworthy recognition of osmotic adjustment as a significant and efficient mechanism for resisting salinity in plants. Under saline environment, a positive growth relationship with osmotic adjustment was found, primarily because of building up more K^+ and glycinebetaine, while a reduction of sugars (Ochiai and Matoh 2001). Correspondingly, Orabi and Abdelhamid (2016) found that salt-tolerant faba bean cultivar "Giza 843" was correlated with a superior capacity of osmotic adjustment by building up proline and ions, e.g., P, K^+, Ca^{2+}, and Mg^{2+}, compared to the salt-sensitive cultivar "Giza 3." Moreover, the salt-tolerant *Phaseolus vulgaris* genotype "RIL115" has been found to have superior osmotic adjustment by building up more soluble sugar, proline, amino acid, and ions, e.g., P, K^+, Ca^{2+}, Mg^{2+}, and Mn^{2+}, compared to the salt-sensitive genotype "RIL147" (Bargaz et al. 2016).

The accumulation of soluble carbohydrates in crops has been commonly recorded as a reaction to salinity (Murakeozy et al. 2003; Dawood et al. 2016). Amino acids were reported to accumulate under salinity stress in higher plants (vascular plants) (Mansour 2000). Di Martino et al. (2003) reported that building up amino acids and glycinebetaine caused osmoregulation, considered one of the predominant methods used by spinach crops to withstand salt stress. Several authors reported that in salt-stressed plants, proline accumulates more than other amino acids (Ashraf 1994; Bekheta et al. 2009; Abdelhamid et al. 2013a; Rady et al. 2016b).

Antioxidant metabolism, including antioxidant enzymes and nonenzymatic compounds, plays a critical role in salinity-induced detoxification of reactive oxygen species (ROS). Salinity tolerance is strongly associated with antioxidant enzyme activity, i.e., catalase (CAT), superoxide dismutase (SOD), glutathione peroxidase (GPX), and ascorbate peroxidase (APX), and nonenzymatic antioxidant, i.e., glutathione reductase (GR) (Gupta et al. 2005; Orabi and Abdelhamid 2016). Moreover, Orabi and Abdelhamid (2016) reported that faba bean plant is protected against the damaging impact of salinity primarily by enhancing the activity of enzymes, e.g., superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), and phenylalanine acid lyase (PAL) enzymes.

It is well established in the literature that salinity causes severe decrease in plant yield. Several studies have already determined the fact that crops are adversely affected by this phenomenon, from planting to harvesting and even in storage. Salinity not only adversely affects seed yield and yield components in many plant species such as lupine (Dawood et al. 2016), common bean (Rady et al. 2016a), wheat (Ouda et al. 2015; Rady et al. 2016a), and faba bean (Orabi and Abdelhamid 2016) but also causes a nutritional imbalance in seed quality in terms of decreasing oil percentage, carbohydrates, and concentrations of 17 amino acids in lupine seeds (Dawood et al. 2016) and decreasing protein content in leaves and oat grains, with increasing level of salt in irrigation water (Kumar et al. 2010). In contrast, salinity raised carbohydrate and protein in seed yield of two faba bean cultivars (Orabi and Abdelhamid 2016) and increased protein, phenolic concentration, and lupine seed alkaloids (Dawood et al. 2016).

3 Techniques Used to Overcome Salt Stress in Plants

Salinity can be limited by salt leaching from the root rhizosphere, altering practices of farm management, and using salt-tolerant plants. Using new irrigation approaches such as deficit irrigation and using irrigation systems such as drip and sprinkler irrigation to optimize water use efficiently can sustain irrigation practices. Farming systems could also be modified to include better crop rotation in order to integrate perennials in crop rotation with annual crops and legumes within rotations and to adopt a precise agricultural approach. While using these tactics to sustainable agriculture that can alleviate the reduction of yields under the stress of salinity, the application is often limited due to the cost and availability of good-quality water or lack of water resources. Hence, developing an efficient, low-cost, easily adaptable technique to enhance plant performance under salt stress is a challenge. Globally, comprehensive study has been carried out to create strategies to deal with the stress of salinity, for example, the development of salt-tolerant varieties. Using organic and inorganic compounds, nutrients, and seed priming is one of the promising strategies adopted to alleviate the unfavorable outcomes of salinity and improve plant yields and yield quality.

3.1 Use of Osmoprotectants, Plant Growth Regulators (PGRs), Vitamins, and Nutrients

Much attention has been given to the approach of using osmolytes, osmoprotectants, plant growth regulators, and plant nutrient supply to overcome plant salt stress and boost crop production under saline conditions. Osmoprotectants or compatible solutes are greatly soluble compounds of low molecular weight, which can accumulate in cells without impairing cellular function at high levels. They safeguard crops against stress by contributing to cellular osmotic adjustment, detoxifying reactive oxygen species (ROS), protecting the structure of membranes, and stabilizing proteins (Ashraf and Foolad 2007). Exogenous use of glycinebetaine (GB) in perennial ryegrass significantly reduces salt stress negative impacts. The suggestion that GB increased salt tolerance in perennial ryegrass was primarily associated with increased SOD, CAT, and APX activity and cell membrane damage alleviation by reducing membrane lipid oxidation and improving ion homeostasis under salt stress (Alasvandyari et al. 2017). Exogenous proline applications alleviated oxidative stress and increased plant growth. Abdelhamid et al. (2013a) reported that proline increased the activity of antioxidant enzymes, superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), as well as carotenoid, ascorbic and endogenous proline, and P and K^+ and K^+:Na^+ concentrations in salt-affected common bean plants. In addition, proline provided osmoprotection and facilitated the growth of salt-stressed faba bean plants (Dawood et al. 2014b). In order to improve their salt tolerance, a number of natural or synthetic PGRs were exogenously applied to crops. A foliar spray of indole-3-acetic acid at 150 ppm, for example, gave the highest plant growth values (flag leaf area and SPAD values), yield (grain and straw yield), and chemical composition (total crude protein, P and K percent) of wheat grown under salt stress conditions (El-Metwally et al. 2015). Khodary (2004) reported a significant increase in growth and development of maize under saline conditions due to applied 0.1 mM of salicylic acid to maize plants. A number of other organic compounds were also exogenously applied to test their effect on the plant's response to saline conditions. In faba bean, for example, Semida et al. (2014) suggested that antioxidant α-tocopherol could activate antioxidants in plants and decrease oxidative damage resulting in physiological modifications in plants grown in saline soil. Furthermore, Dawood et al. (2016) concluded that the damaging impacts of salt stress on lupine plant growth and seed yield nutritional value were to some extent alleviated, mainly at 200 ppm α-tocopherol. In soybean, Rady et al. (2015) reported that 100 mg L^{-1} α-tocopherol exogenous application increased net assimilation rate, relative growth rate, chlorophyll, proline, free amino acids, soluble sugars, N, P, K^+, and K^+:Na^+ ratios in soybean plants under salt stress. Exogenous use of 200 or 400 mg l^{-1} nicotinamide (vitamin B3) increased the nutrient concentration, sucrose, soluble sugars, free amino acids, lipid peroxidation, oxidative enzymes, photosynthetic pigments, plant growth, and seed yield and improved the quality of the seed yield, i.e., carbohydrates and protein of faba bean salt-stressed plants (Abdelhamid et al. 2013b).

Amino acids are well-known biostimulants that affect plant growth and yield positively, thus mitigating abiotic stress injuries significantly. For example, amino acid mixture on faba bean has been reported to have increased shoot length, leaf number per plant, fresh and dry shoot weight, photosynthetic pigments, total carbohydrates, polysaccharides, DNA, and nucleic acid RNA (Sadak et al. 2015). In addition, amino acid exogenous foliar application at rate of 500 or 1000 or 1500 mg L^{-1} enhanced salt tolerance of faba bean plants by increasing osmotic solutes, phenolic content, IAA, and endogenous polyamine content, while it reduced antioxidant enzymes and lipid peroxidation (Sadak and Abdelhamid 2015).

Salt-induced nutritional disorders can be alleviated by adding mineral nutrients to the growth medium, according to numerous reports. Adding N, for example, has improved growth and yield of sorghum crop (Esmaili et al. 2008). In addition, Rady et al. (2016b) recommended use of $^{1}/_{3}\,H_4NO_3$ at rate of 55 kg N ha^{-1} + cerealine (at rate of 4 kg ha^{-1} bio-fertilizer) + cattle manure (at rate of 10 t ha^{-1}) in saline soils to improve wheat growth and nutritional yield quality with reduced heavy metal content. Also, in wheat, El-Lethy et al. (2013) reported important increases in photosynthetic pigments, antioxidant enzyme activity, soluble sugar, starch and total phenols, N, P, K^+, and K^+:Na^+ ratio and wheat grain yield due to soil application of 150 mg K_2O kg^{-1}. It was also concluded that 150 mg K_2O kg^{-1} soil reduced the unfavorable effects of NaCl salinity by enhancing photosynthetic pigments, antioxidant enzyme activity, osmoprotectant concentrations, and K^+:Na^+ ratio, which all were reflected in increasing the growth of common bean plants (Dawood et al. 2014a). Bargaz et al. (2016) found major increase in P, K^+, Ca^{2+}, and Mg^{2+} in leaves of both common bean recombinant inbred lines (RILs) and noteworthy increase in chlorophyll, carotenoids, soluble sugars, free amino acids and proline, and seed yields in all salinity intensities up to 60 kg ha^{-1} P. Like P, it is known that calcium (Ca) improves the unfavorable effects of salinity in plants, most probably by making possible superior selectivity of K^+:Na^+ ratios (Hasegawa et al. 2000). Foliar fertilization is generally a useful technique for supplementing plant-deficient nutrients when soil conditions restrict the availability of nutrients to roots (Mengel 2002). Under saline conditions, the absorption of K, Ca^{2+}, and N through the roots and their supply to growing shooting regions is significantly impaired (Munns 2005), and thus the plant's optimum concentration of essential nutrients is reduced (Marschner 1995). In this case, foliar fertilization can be used to promote mineral nutrition, suppress physiological disorders, and promote growth and yield of plant (Pervez et al. 2004). Efficiency of foliar applied nutrients depends on their mobility within the plant (Mengel 2002). Of all nutrients, N, K, and Mg are more phloem-mobile, whereas Ca and Fe are least phloem-mobile. Thus, foliar application of the latter two nutrients is not effective (Mengel 2002).

3.2 *Seed Priming*

Proof of seed priming benefits has been reported extensively. Seed priming is a water-based method that allows regulated seed rehydration to activate the generally activated metabolic classes during early germination but stops the transition of seed into complete germination. Priming is commonly used to treat vegetable seeds, mainly carrots, leek, onions, tomatoes, peppers, cucumbers, broccoli, lettuce, and okra (Dearman et al. 1987; Mahmoudi et al. 2012; Demirkaya 2014; Azooz et al. 2015; Hassini et al. 2017; Sarwar et al. 2017; Rinez et al. 2018), and field crop seeds, mostly wheat, canola lentil, alfalfa, bean, mung bean, common bean, safflower, barley, and maize (Jabeen and Ahmad 2013; Jamil et al. 2012; Al-Tawaha and Al-Ghzawi 2013; Azooz et al. 2013; Movaghatian and Khorsandi 2014; Younesi and Moradi 2014; Ali et al. 2017; Keshavarza and Moghadam 2017; Imran et al. 2018; Tabassum et al. 2018). Priming helps improve the quality of the product in flower seed industry that is usually utilized in best cultivars of *Petunia* (Momin 2013). Herbs, such as ajwain, dill, wild foxglove, rosemary, and scarlet sage, as well enjoy seed priming (Di Girolamo and Barbanti 2012; Mahdavi and Rahimi 2013; Ghassemi-Golezani and Nikpour-Rashidabad 2017; Masondo et al. 2018). Priming has also been used on *Arabidopsis thaliana*, which is the preferred model system for plant biology research (Jiménez-Arias et al. 2015). In seed conditioning in agriculture, several seed priming techniques have been successfully used to accelerate germination rates, improve seed uniformity, and improve yield and yield quality such as hydropriming, osmopriming, and halopriming (e.g., Jabeen and Ahmad 2013; Mahmoudi et al. 2012; Ouhibi et al. 2014; Maswada and Abd El-Kader 2016; Masondo et al. 2018; Panuccioa et al. 2018; Tabassum et al. 2018). Seed priming also promotes many plants to neutralize environmental stress negative impacts, such as salinity stress (see references in Table 1). A growing research has discussed and provided an outline of seed priming expertise, summarizing the currently available physical, chemical, and biological treatments (see recent reviews, e.g., Paparella et al. 2015; Ibrahim 2016; Mahmood et al. 2016). The following is a brief outline of seed priming methods:

Table 1 The functions of seed priming in plant under salt stress

Plant species	Priming agent/concentration/time	Main findings	References
Tomato (*Solanum lycopersicum*)	Menadione sodium bisulfite/1.3 mg L^{-1}	Improved net photosynthesis, regulated stomatal aperture and maintained water balance, and increased relative growth rate	Jiménez-Arias et al. (2019)
	NaCl/0.05 M	Increased germination, root length, hypocotyl lengths, fresh weights, proline, and anthocyanin	İşeri et al. (2014)
	NaCl/5 M	Increased chlorophyll content, Na, K^+, Ca, Mg, and soluble sugars	Demirkaya (2014)
Chickpea (*Cicer arietinum*)	Mannitol/2 and 4%/24 h	Increased plant survival and growth	Sarwar et al. (2006)

(continued)

Table 1 (continued)

Plant species	Priming agent/concentration/time	Main findings	References
Pepper (*Capsicum annuum* L.)	Aqueous extracts of *Padina pavonica*/60 g L^{-1} or *Jania rubens*/80 g L^{-1}	Increased proline, total soluble sugar, K, and P, while reduced leakage of electrolytes and MDA content	Rinez et al. (2018)
Maize (*Zea mays* L.)	Deionized water/24 h or $ZnSO_4$ $7H_2O$/4 mM/24 h	Increased biomass production, nutrient status, and early seedling development	Imran et al. (2018)
	Distilled water or leaf extracts of *Rosmarinus officinalis* or *Artemisia*	Increased germination, photosynthetic pigments, chlorophyll fluorescence, photosynthetic efficiency, and antioxidant system	Panuccioa et al. (2018)
	Magnetic fields (MF)/week (15 mT) or strong (150 mT)	Enhanced rate and percentage of germination and improved plant growth	Karimi et al. (2017)
	Tap water or salicylic acid/0.5 mM or NaCl/2 dS m^{-1}	Increased CAT, SOD, peroxidase, soluble proteins, K, rate of emergence and colonization %, while Na^+ decreased	Kazemi et al. (2018)
Z. mays, *P. sativum*, and *L. sativus*	Gibberellic acid/0.2 g L^{-1}/12 h	Increased percentage of germination, length of shoot and root, and total crop weight, while reduced time for germination	Tsegay and Andargie (2018)
Rice (*Oryza sativa*)	Gibberellic acid/0, 50, 100 and 150 ppm	Increased germination, seedling growth, and weight, while decreased toxic ions such as Na^+	Imran et al. (2016)
	Validamycin A/30 μM	Increased grain yield, weight of 1000 grains, and percentage of filled grain, while decreased trehalose activity, leading to accumulation of trehalose	Hathout et al. 2014
Barley (*Hordeum vulgare*)	dH_2O or $CaCl_2$/1.5% or *Enterobacter* spp. strain FD17	Improved leaf area, grain yield, harvest index, chlorophyll a, chlorophyll b, total soluble phenolics, proteins, proline, glycine betaine, K^+, relative water content, osmotic and pressure potential, and stability of the cell membrane while decreased MDA and Na^+	Tabassum et al. (2018)

(continued)

Table 1 (continued)

Plant species	Priming agent/concentration/time	Main findings	References
Sorghum (*Sorghum bicolor*)	PEG-6000/-0.86 Mpa/48 h	Increased activities of catalase (CAT) and guaiacol peroxidase (POX)	Oliveira et al. (2012)
	PEG-6000/-0.86 Mpa/48 h	Increased proline, while reduced Na^+ and Cl^-	Oliveira et al. (2011)
	PEG-6000/-0.86 Mpa/48 h	Increased root growth	Patanè et al. (2009)
Safflower (*Carthamus tinctorius*)	Glycine betaine/0, 10, 30, and 60 mM	Increased enzyme activities (CAT, SOD), cell membrane stability, K^+, and protein, while reduced peroxidase, MDA, and Na^+:K^+ ratio	Alasvandyari et al. (2017)
	Chitosan/0, 0.25, 0.50, and 0.75% dissolved in 1% acetic acid/3 h	Increased germination %, while decreased MDA, proline, and activity of CAT and POX	Jabeen and Ahmad (2013)
Sunflower (*Helianthus annuus*)	KNO_3/-1.0 M Pa/24 h	Increased percentage of germination, radicular length, height of seedling, biomass, leaf number, and K^+	Bajehbaj (2010)
Dill (*Anethum graveolens*)	Gibberellic acid/1 mM/4 h or salicylic acid/1 mM/4 h	Increased ratio of K^+:Na^+, osmolytes (i.e., proline, glycine betaine, soluble sugars), enzymes (i.e., SOD, APX, POX), production of essence, and yield of essential oil	Ghassemi-Golezani and Nikpour-Rashidabad (2017)
Cucumber (*Cucumis sativus*)	Triacontanol/25 and 50 μM/12 h	Increased seedling emergence rate, uniformity and early growth, shoot and root length, dry weight seedling, chlorophyll, proline, and exchange gas traits	Sarwar et al. (2017)
Broccoli sprouts (*Brassica oleracea*)	KCl/50 mM	Increased water relation traits (i.e., osmotic and water potential and hydraulic root conductivity) and glucosinolate	Hassini et al. (2017)
Pea (*Pisum sativum*)	Leaf extracts of *Typha angustifolia*/40 g L^{-1}/48 h (seed weight/volume; 1:5 (w/v))	Increased germination%, osmotic (proline, soluble sugars, K^+, P), chlorophyll, carotenoid, secondary metabolites (total phenolic, total flavonoid), while reduced electrolyte leakage and MDA	Ghezal et al. (2016)

(continued)

Table 1 (continued)

Plant species	Priming agent/concentration/ time	Main findings	References
Mung bean (*Vigna radiata*)	β-Amino butyric acid/0, 0.5, 1.0, 1.5, 2.0, and 2.5 mM/6 h	Increased fluorescence chlorophyll a, proline, protein, carbohydrate, nitrate reductase, and antioxidant enzymes of POX and SOD, photosynthetic pigments, activity of photosynthetic and mitochondrial while decreased MDA	Jisha and Puthur (2016)
	Salicylic acid (SA)/0, 0.00001, 0.001, and 10 mM/6 h	Increased germination %, germination rate, radicle length, plumule length, and vigor index. SA with 0.00001 mM is recommended	Movaghatian and Khorsandi (2014)
Okra (*Hibiscus esculentus*)	Jasmonate/50 μM solution for 10 h	Increased fresh weight, dry weight, water content, chlorophyll, relative water content, osmoprotectants (soluble sugars, soluble proteins, proline), mineral (K^+, Ca^{2+}, Mg^{2+}), K^+:Na^+ and Ca^{2+}:Na^+ ratios, membrane stability index, antioxidant enzyme (POD, APX), while reduced Cl^-, Na^+, H_2O_2, and MDA	Azooz et al. (2015)
Arabidopsis (*Arabidopsis thaliana*)	Menadione sodium bisulfite/2, 20, and 40 mM/2 d	Increased dry and fresh weight, relative rate of growth, and proline	Jiménez-Arias et al. (2015)
Broad bean (*Vicia faba* L.) seeds	Salicylic acid/0.2 mM/10 h	Increased growth (i.e., dry root, shoot weight, leaf area), water relations (i.e., plant water content, leaf relative water content), osmotic solutes (i.e., soluble carbohydrate, protein, amino acids), enzymes (i.e., CAT, POD, APX, GR), and ascorbic acid while decreased MDA and EC percentage	Azooz (2009)
Alfalfa (*Medicago sativa*)	Gibberellic acid/0, 3, 5, and 8 mM/24 h	Increased germination rate, dry weight, enzyme activity (SOD, CAT, POX, APX), and ascorbate, while reduced membrane permeability (electrolyte leakage) and MDA	Younesi and Moradi (2014)

(continued)

Table 1 (continued)

Plant species	Priming agent/concentration/time	Main findings	References
Lettuce (*Lactuca sativa*)	dH_2O/2 h or KNO_3/0.5%/2 h Gibberellic acid/3 mM/12 h	Increased dry weight of leaves, number of leaves, area of leaves, leaf water, chlorophyll, carotenoids, enzymes (CAT, GPX), ascorbate, while decreased leakage of electrolytes	Mahmoudi et al. (2012)
Chinese cabbage (*B. oleracea capitata*)	dH_2O/10 h or gibberellic acid/100, 150, and 200 mg L^{-1}/10 h	Increased seed water uptake, germination rate, leaf area, chlorophyll, relative water content, fresh and dry weights, membrane stability, while decreased electrolyte leakage	Jamil et al. (2012)
Melon (*Cucumis melo*)	NaCl/18 dS m^{-1}/3 d	Increased stomatal conductance, chlorophyll, fruit set, K^+ leaf and stem, Ca leaf and stem, while reduced Na^+ leaf and stem	Sivritepe et al. (2005)
Sugarcane (*Saccharum officinarum*)	NaCl/100 mM	Increased germination %, rate of germination, and shoot length	Patade et al. (2009)
Wheat (*Triticum aestivum*)	Sodium nitroprusside (a nitric oxide donor)/0, 0.1, and 0.2 mM/12 h	Increased shoot and root biomass, shoot length, 100 grain weight, grain yield, antioxidant enzymes (i.e., SOD, POD, CAT), ascorbic acid, proline, and total phenolics, while deceased H_2O_2 and MDA	Ali et al. (2017)
	dH_2O or $CaCl_2$/1.5% /12 h (seed to solution ratio 1:5 (w/v)	Increased area of the leaf, water relations, proline, glycine betaine, and yield of grain while decreased MDA and Na^+	Tabassum et al. (2017)
	dH_2O or KCl/100 mM or $CaCl_2$/100 mM	Increased proline, phenolic compounds, antioxidant enzyme activities (CAT, POD, APX), while reduced H_2O_2 and MDA	Islam et al. (2015)
	Chilling/3 °C/2 weeks	Increased net photosynthetic rate, growth, yield greater, root, K^+, and Ca^{2+}, while reduced Na^+ in the shoots	Iqbal and Ashraf (2010)
	$CaCl_2$/50 mM/12 h or NaCl/50 mM/12 h or $CaSO_4$/50 mM/12 h	Increased germination, length of root, fresh and dry weights, and K^+. The most effective priming agents were $CaSO_4$ and $CaCl_2$	Afzal et al. (2008)

3.2.1 Hydropriming

In hydropriming, seeds are soaked in water with or without aeration at optimum temperature (generally on or after 5–20 °C) and regularly for 6–24 h. This method is especially helpful in rural regions where crop production is damaged by unfavorable climatic environments, e.g., drought, and is required to enhance the efficiency of water use by decreasing chemical exposure (McDonald 2000). Hydropriming has long been known for its advantages, although it is now used less frequently than other methods. Harris (1992) suggested hydropriming as an inexpensive practice, explained for several crops in developing countries as “on-farm seed priming.”

3.2.2 Osmopriming

Osmopriming is known as osmotic priming or osmotic conditioning as well. It is a common pre-sowing practice that uses low-water-potential osmotic solutions to help manage water uptake. Osmopriming’s main goal is to limit the oxidative damage caused by ROS by preventing water from entering. As a result, the osmotic agent’s water potential is a critical factor (Heydecker and Coolbear 1977; Taylor et al. 1998). In osmopriming, seeds are soaked in osmotic agent solutions for a certain time period.

This technique mainly utilizes sugars, polyethylene glycol (PEG), glycerol, sorbitol, or mannitol, followed by air drying pre-sowing.

3.2.3 Solid Matrix Priming

The priming of solid matrix is also known as “matriconditioning.” It has been developed as a replacement to avoid high osmopriming costs, which require big volumes of osmotic solution and costly temperature management and aeration systems (Paparella et al. 2015). There are a number of natural materials that were used for solid priming as matrices, e.g., charcoal, sawdust, coal, calcined kaolin, and vermiculite, and marketable materials, e.g., Agro-Lig®. Solid matrix priming is best performed in an air circulation sealed container while avoiding too much evaporation.

3.2.4 Biopriming

Biopriming is a method using a combination of useful or bioactive particles. Is it well acknowledged that the mixture of plants with particular fungi or bacteria yields very appropriate outcomes as these microorganisms are capable of creating endophytic connections with the plant, leading to enhanced plant development and manufacturing of phytohormones and enhanced biotic/abiotic stress resistance (Waller et al. 2005). *Bacillus* spp., *Enterobacter* spp., *Pseudomonas* spp., and *Trichoderma* spp. are the most frequently used biopriming species (Niranjan Raj et al. 2004). In addition, biopriming is accomplished by adding secondary metabolites to the priming mixture and phytohormones (Hamayun et al. 2010).

3.2.5 Chemopriming

By addition of conventional decontaminators like sodium hypochlorite (NaOCl), hydrochloric acid (HCl), natural substances, and agrochemicals (e.g., herbicides, insecticides, fungicides, fumigants) to the priming solution for microbial pollution prevention, Chemopriming is accomplished (Parera and Cantliffe 1990). Natural compounds with a wide range of antimicrobial activity, including organic acids, essential oils, crude extracts of plants, and milk products, are mainly used for seed disinfection in organic farming (Van der Wolf et al. 2008). Additional environmentally acceptable means such as those made from insecticidal and fungicidal microencapsulated plant extracts are being tested (Gaidau et al. 2014).

3.2.6 Thermopriming

Thermopriming is a technique that seeds subject to different temperatures before sowing. This practice has been widely demonstrated to enhance germination effectiveness under negative environmental circumstances, decreasing seed germination thermo-inhibition (Huang et al. 2002). Thermopriming is accomplished by presowing seed at different temperatures.

4 Mechanisms Induced by Seed Priming to Increase Plant Tolerance to Salt Stress

Seed priming has been shown to increase germination percentage, shoot and root length, shoot to root ratio, shoot to root weight, germination percentage, germination time, radicular length, radicular surface area, average radicle and radicle volume diameter, germination stress tolerance, seedling vigor, shoot and root length stress, fresh and root weight, and germination speed (Patade et al. 2009; Bajehbaj 2010; Movaghatian and Khorsandi 2014; Ghezal et al. 2016; Al-Tabbal 2017; Nimac et al. 2018); increased photosynthetic pigments in terms of chlorophyll, carotenoids, and chlorophyll fluorescence (Anwar et al. 2011; Demirkaya 2014; Azooz et al. 2015; Ghezal et al. 2016; Jisha and Puthur 2016; Abdel Latef et al. 2017; Panuccioa et al. 2018; Tabassum et al. 2018); increased plant water content (relative water content, osmotic and water potential, and root hydraulic conductivity) (Azooz 2009; Jamil et al. 2012; Ouhibi et al. 2014; Hassini et al. 2017; Tabassum et al. 2017; Yang et al. 2017; Jiménez-Arias et al. 2019); improved leaf photosynthetic rate and stomatal conductance (Iqbal and Ashraf 2013; Jisha and Puthur 2016; Sarwar et al. 2017; Yang et al. 2017; Panuccioa et al. 2018; Jiménez-Arias et al.

2019); increased osmoprotectants (soluble sugars, soluble proteins, and proline) (Oliveira et al. 2011; Jabeen and Ahmad 2013; Azooz et al. 2015; Abdel Latef et al. 2017; Ghassemi-Golezani and Nikpour-Rashidabad 2017); increased enzymatic antioxidant activity, i.e., catalase (CAT), peroxidase (POX), superoxide dismutase (SOD), ascorbate peroxidase (APX), and glutathione reductase (GR) (Azooz 2009; Jabeen and Ahmad 2013; Oliveira et al. 2012; Abdel Latef et al. 2017; Alasvandyari et al. 2017; Mekawy et al. 2018); increased nutrient uptake, i.e., K^+, Ca^{2+}, and Mg^{2+} (Afzal et al. 2008; Iqbal and Ashraf 2010; Anwar et al. 2011; Demirkaya 2014; Azooz et al. 2015); increase plant growth (relative growth rate, unit leaf rate, leaf area ratio, specific leaf area) (Maswada and Abd El-Kader 2016); enhanced organic solutes, i.e., soluble sugar, soluble protein, free amino acids, proline, and betaine (Anwar et al. 2011; Oliveira et al. 2011; Azooz et al. 2015; Jiménez-Arias et al. 2015; Ghezal et al. 2016; Jisha and Puthur 2016; Alasvandyari et al. 2017; Ghassemi-Golezani and Nikpour-Rashidabad 2017; Sarwar et al. 2017; Keshavarza and Moghadam 2017; Tabassum et al. 2017); reduced leakage of electrolytes and H_2O_2 content and MDA content (Jisha and Puthur 2014; Alasvandyari et al. 2017; Mekawy et al. 2018; Rinez et al. 2018; Tabassum et al. 2018); and consequently increased plant yield (biomass, grain yield, yield attributes) (Iqbal et al. 2006; Iqbal and Ashraf 2010, 2013; Mohammadi et al. 2012; Ghezal et al. 2016) and accordingly is capable to boost plant performance and tolerance under salinity stress in several crops such as okra (Azooz et al. 2015), wheat (Iqbal and Ashraf 2010; Maswada and Abd El-Kader 2016), quinoa (Yang et al. 2017), and pepper (Rinez et al. 2018).

Table 1 shows the functions of seed priming in plant under salt stress. In Table 1, there are many plant species that were tested for seed priming under salt stress, namely, tomato (*Solanum lycopersicum*), sea fennel (*Crithmum maritimum* L.), quinoa (*Chenopodium quinoa* Willd.), chickpea (*Cicer arietinum*), pepper (*Capsicum annuum* L.), maize (*Zea mays* L.), rice (*Oryza sativa* L.), *barley* (*Hordeum vulgare*), wild foxglove (*Ceratotheca triloba*), sorghum (*Sorghum bicolor*), safflower (*Carthamus tinctorius* L.), sunflower (*Helianthus annuus* L.), lupine (*Lupinus termis*), dill (*Anethum graveolens* L.), cucumber (*Cucumis sativus*), broccoli sprouts (*Brassica oleracea*), common bean (*Phaseolus vulgaris*), pea (*Pisum sativum* L.), mung bean (*Vigna radiata* L.), okra (*Hibiscus esculentus*), *Arabidopsis* (*Arabidopsis thaliana*), faba bean (*Vicia faba* L.), alfalfa (*Medicago sativa*), lettuce (*Lactuca sativa*), lentil (*Lens culinaris*), Chinese cabbage (*B. oleracea capitata*), canola (*Brassica napus*), melon (*Cucumis melo*), sugarcane (*Saccharum officinarum* L.), ajwain (*Carum copticum*), and wheat (*Triticum aestivum* L.). These plant species were tested for seed priming techniques using many materials with different concentrations, namely, distilled water (dH_2O), menadione sodium bisulfite ($C_{11}H_9NaO_5S$), gibberellic acid ($C_{19}H_{22}O_6$), saponin ($C_{36}H_{58}O_9$), zinc sulfate ($ZnSO_4$), salicylic acid ($C_7H_6O_3$), apigenin ($C_{15}H_{10}O_5$), validamycin A ($C_{20}H_{35}NO_{13}$), phloroglucinol ($C_6H_6O_3$), polyethylene glycol 6000 (*PEG-6000*) ($HO(C_2H_4O)_nH$), glycine betaine ($C_5H_{11}NO_2$), chitosan ($C_{56}H_{103}N_9O_{39}$), acetic acid ($C_2H_4O_2$ or CH_3COOH), potassium nitrate (KNO_3), zinc oxide (ZnO nanoparticles), triacontanol ($C_{30}H_{62}O$), vitamin B12 ($C_{63}H_{88}CoN_{14}O_{14}P$), zinc sulfate ($ZnSO_4$), β-amino butyric acid ($C_4H_9NO_2$), jasmonic acid ($C_{12}H_{18}O_3$), ascorbic acid (vitamin C) ($C_6H_8O_6$ or $HC_6H_7O_6$), nicotinamide (vitamin B3) ($C_6H_6N_2O$), sodium nitroprusside ($Na_2[Fe(CN)_5(NO)]$), kinetin ($C_{10}H_9N_5O$), indole acetic acid ($C_{10}H_9NO_2$), indolebutyric acid ($C_{12}H_{13}NO_2$), tryptophan ($C_{11}H_{12}N_2O_2$), calcium sulfate ($CaSO_4$), calcium chloride ($CaCl_2$), potassium chloride (KCl), sodium chloride (NaCl), putrescine ($C_4H_{12}N_2$), spermidine ($C_7H_{19}N_3$), spermine ($C_{10}H_{26}N_4$), Zn-glutamine ($C_5H_{10}N_2O_3$), Zn-glycine ($C_4H_8N_2O_4Zn$), Zn-arginine ($C_6H_{14}N_4O_2$), and Zn-histidine ($C_6H_9N_3O_2Zn$), UV-C irradiation, *Enterobacter* spp. strain FD17, magnetic fields, aqueous extracts of *Padina pavonica* or *Jania rubens* or *Typha angustifolia* or *Rosmarinus officinalis* or *Artemisia*, commercial seaweed extract, and smoke-compound karrikinolide.

It has also been previously documented that plants are constructing many physiological and biochemical adaptations to adjust themselves under saline environments. With regard to using seed priming to alleviate the salt stress effects on plants, we proposed a schematic diagram describing the chain reaction following the seed priming (Fig. 2). The diagram illustrates the possible impact of the seed priming on different physiological processes, enhancing tolerance level and final yield.

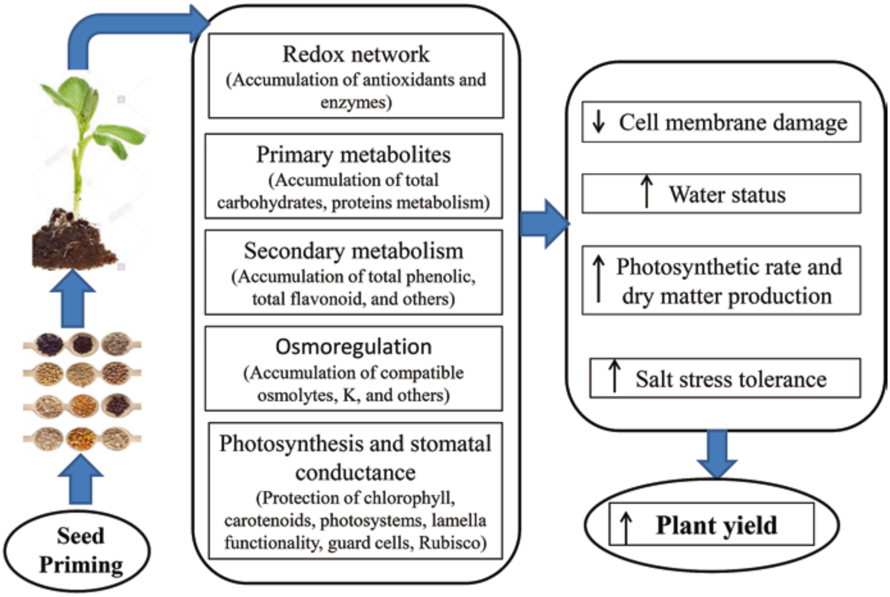

Fig. 2 Schematic diagram describing the chain reaction following the seed priming. The diagram illustrates the possible impact of the seed priming on different physiological processes, enhancing tolerance level and final yield

4.1 Induced Salt Tolerance by Seed Priming Through Plant Physiological Response

Photosynthesis is the biochemical pathway through which plants transform solar energy into the chemical energy needed for growth. Under salt stress, reduced photosynthetic rates in plants are primarily due to reduced water potential and/or greater of Na^+ and/or Cl^- in chloroplasts that slow down chlorophyll (Iqbal and Ashraf 2007; Khayyat et al. 2014). Reducing the content of chlorophyll is common under salt stress and has been used in many reports as a sensitive indicator for cell metabolism (Chutipaijit et al. 2011). Reductions in chlorophyll a, chlorophyll b, carotenoids, and photosynthetic pigments have been recorded in faba bean following 44-day use of diluted seawater with 3.13 or 6.25 dS m^{-1}, with reduced total pigments by 6.7% and 15.6%, respectively, using both seawater treatments compared to control crops (Dawood et al. 2014b). In another study in soybean plants that are exposed to diluted salinity of seawater, chlorophyll a, chlorophyll b, total carotenoids, and total concentrations of pigments gradually decreased with increased levels of salt stress (Rady et al. 2015). Membrane deterioration is considered one of several reasons which might affect negatively on the chlorophyll under stress (Mane et al. 2010). Moreover, increased chlorophyll a and chlorophyll b content was reported by Tabassum et al. (2018), which was correlated with increased cell membrane stability.

Photosystem II (PS II), when subjected to salt stress, is a fragile component of the photosynthetic structure (Allakhverdiev et al. 2000). The efficiency of PS II, the electron transportation chain (ETC), and the net rate of CO_2 assimilation have been reported to be reduced under salt stress (Piotr and Grazyna 2005). Moreover, changes in *Scenedesmus obliquus*' photosynthetic attributes resulting in reduced biomass accumulation were reported (Demetriou et al. 2007). There was no significant difference in salt tolerant-cultivar *Vicia faba* cv. Giza 843 a susceptible one Giza 4 under the saline condition in Fv/Fm (used to estimate PS II's potential efficiency through darkly adapted measurements), while Giza 843 had a significantly higher PI (photosynthetic performance index) (Semida et al. 2014). Salt stress decreased the development of citrus by decreasing the net photosynthetic rate, stomatal behavior, PS II performance, and photosynthetic efficiency (Lòpez-Climent et al. 2008). It has been reported that salinity stress affects barley growth by altering chlorophyll fluorescence (PS II) and developing complex oxygen functions (Kalaji et al. 2011). In addition, salt stress decreased *Brassica* development by influencing PS II, electron transport rates, and D1 protein (Mittal et al. 2012). Moreover, under salt stress, there are other reasons that reduce net CO_2 assimilation rates, such as cell membrane dehydration, which decreases carbon dioxide permeability, salt toxicity, increased senescence, variations in cytoplasmic structure-induced enzyme activity, and negative reaction to decreased sink activity (Iyengar and Reddy 1996).

As discussed above, a plant under salt stress faces a reduction in photosynthetic rates due to a decreasing in water potential accompanied/or not with too much concentration of Na^+ and/or Cl^- in the chloroplasts and chlorophyll. Therefore, any means that could increase plant water potential and exclude Na^+ and Cl^- may increase chlorophyll content and improve photosynthetic performance of PS II and consequently result in enhancing net CO_2 photosynthetic rate and finally boost plant yield. In this regard, several authors reported that seed priming materials (e.g., saponin; dH_2O; $CaCl_2$; zinc nanoparticles (ZNPs); vitamin B12; NaCl; indole acetic acid; indolebutyric acid; tryptophan) increased photosynthetic pigment (chlorophyll *a*, chlorophyll *b*, carotenoids), photosystem II, and net CO_2 photosynthetic rate in several crops, e.g., quinoa, *barley*, lupine, common bean, mung bean, and wheat (Jisha and Puthur 2014; Abdel Latef et al. 2017; Keshavarza and Moghadam 2017; Yang et al. 2017; Tabassum et al. 2018). More details about the materials used for priming and their concentrations are shown in Table 1. A schematic diagram describing the chain reaction following the seed priming is shown in Fig. 2. The diagram illustrates the possible impact of the seed priming on different physiological processes, enhancing tolerance level and final yield.

It was reported that improved photosynthetic pigment (chlorophyll *a*, chlorophyll *b*, carotenoids), photosystem II, and net CO_2 assimilation rate by seed priming application ($CaCl_2$; ZNPs; vitamin B12; aqueous leaf extracts of *Typha angustifolia*; β-amino butyric acid; NaCl; jasmonate sodium nitroprusside) were associated with decreased malondialdehyde and hydrogen peroxide in plants under salt stress (Jisha and Puthur 2014, 2016; Azooz et al. 2015; Ghezal et al. 2016; Maswada and Abd El-Kader 2016; Abdel Latef et al. 2017; Keshavarza and Moghadam 2017; Tabassum et al. 2018). Various studies (e.g., Sivritepe et al. 2005; Iqbal and Ashraf 2010; Azooz et al. 2013, 2015; Maswada and Abd El-Kader 2016; Ghezal et al. 2016; Tabassum et al. 2018) reported that enhanced photosynthetic pigment (chlorophyll *a*, chlorophyll *b*, carotenoids), photosystem II, and net CO_2 photosynthetic rate by seed priming application ($CaCl_2$; chilling at 3 °C; NaCl; sodium nitroprusside; diluted seawater with 9.00 dS m^{-1}; ascorbic acid; nicotinamide; jasmonate; aqueous leaf extracts of *Typha angustifolia*) were associated with increased contents of nutrients (P, K^+, Ca^{2+}, Mg^{2+}, $Ca^{2+,}$ Zn), raised Ca^{2+}:Na^+ and K^+:Na^+ ratios, and reduced Na^+ and Cl^- in plants under salt stress. Enhanced photosynthetic pigment (chlorophyll *a*, chlorophyll *b*, carotenoids), photosystem II, and net CO_2 photosynthetic rate by seed priming application ($CaCl_2$; NaCl; ZNPs; jasmonate; ascorbic acid; nicotinamide; EC 9.00 dS m^{-1}; sodium nitroprusside) were correlated with increased organic solute content (proline and glycinebetaine, free amino acids, soluble sugar, soluble protein) under salt stress (Anwar et al. 2011; Azooz et al. 2013, 2015; Jisha and Puthur 2014; Maswada and Abd El-Kader 2016; Abdel Latef et al. 2017; Tabassum et al. 2018). Increased photosynthetic pigment (chlorophyll *a*, chlorophyll *b*, carotenoids), photosystem II, and net CO_2 photosynthetic rate by seed priming application (ZNPs; vitamin B12; aqueous leaf extracts of *Typha angustifolia*; jasmonate; KNO_3; dH_2O; gibberellic acid) were associated with increased enzymatic antioxidants (SOD, CAT, POD, and APX, POX) and nonenzymatic antioxidants (total phenols, flavonoids, ascorbic acid, total carotenoids) in salt-stressed plants (Mahmoudi et al. 2012; Azooz et al. 2015; Ghezal et al. 2016; Abdel Latef et al. 2017; Keshavarza and Moghadam 2017).

4.2 Induced Salt Tolerance by Seed Priming Through Ionic Balance

When plants are stressed by salt, the absorption of essential mineral elements is interrupted. The increase in concentration of Na^+ in the root rhizosphere directly affects negatively on the absorption of many necessary elements, such as K^+, while Na^+ shows opposite correlation with K^+ (Kohler et al. 2009). In most plant species, salt tolerance was correlated with only tiny quantities of Na^+ and Cl^- in the shoots (Greenway and Munns 1980), while Cl^- under saline conditions is the most prevalent anion. Noble and Rogers (1992) proposed shoot Cl^- levels as selection standard for salt tolerance. For instance, in four *Vicia faba* cultivars, Abdelhamid et al. (2010) recorded a partial ion exclusion mechanism, stating that partial toxic ion exclusion was suggested as the main selection parameter for faba bean salt tolerance. They reported that faba bean salt-tolerant cultivars (Giza 429, Giza 843, Misr 1) had higher N, P, K^+, Ca^{2+}, and Mg^{2+} than susceptible cultivars (Giza 3), which showed lesser K^+, Ca^{2+}, and Mg^{2+} while higher Na^+ and Cl^-. Ions' uptake in plants can be exploited as a marker of salt tolerance since they are genetically controlled but also influenced by the environment (Chaubey and Senadhira 1994). The *Vicia faba* salt-tolerant cultivar Giza 429 has been confirmed by Semida et al. (2014) that it had higher levels of N, P, K^+, and Ca^{2+}, whereas susceptible salt cultivar Giza 40 had lower levels of N, P, K^+, and Ca^{2+} but higher levels of Na^+. Furthermore, under saline conditions, high Na^+:K^+ and Na^+:Ca^{2+} ratios occur in the soil due to excessive amounts of exchangeable Na^+. Thus, plants grown in such environments have elevated Na^+ levels, while K^+ and Ca^{2+} take-up is decreased. For the integrity and functioning of cell membranes, rational quantities of both K+ and Ca^{2+} are requisite (Wenxue et al. 2003). For several major metabolic processes in plant cells, optimal K^+ is essential (Tomar and Agarwal 2013). A good amount of K^+:Na^+ and Ca^{2+}:Na^+ ratios are also considered beneficial in maintaining ion balance in plant leaves and demonstrating salt tolerance in plant (Abdelhamid et al. 2010; Semida et al. 2014). Semida et al. (2014) confirmed that *Vicia faba* cv. Giza 429 salt-tolerant cultivar had higher K^+:Na^+ and Ca^{2+}:Na^+ ratio, while susceptible salt cultivar Giza 40 had lower ratios. In addition, Bargaz et al. (2016) reported that *Phaseolus vulgaris* recombinant inbred lines (RIL) RIL115, exhibited more salt tolerance with greater uptake of P, K^+, Ca^{2+}, Mg^{2+}, and Mn^{2+} and higher uptake of K^+:Na^+ than susceptible salt tolerance of RIL147. However, contradictory results for different plant species were reported, where Ashraf et al. (1994) questioned ion exclusion mechanism validation. Moreover, salt-tolerant and salt-sensitive lines were found to vary a little in Na^+ and Cl^- shoot of the species *Atylosia* (Subbarao et al. 1990).

There are several reports examining how seed priming is affecting plant growth and mechanisms involved to help a plant to be more tolerant under salt stress condition. As discussed above that a plant under salt stress with greater elemental contents, i.e., K^+ and Ca^{2+}, and lower Na^+ could be considered salt tolerant. In this regard, several authors reported that seed priming (namely, NaCl, $CaCl_2$, gibberellic acid, PEG-6000, SA, glycinebetaine, $ZnSO_4$, aqueous leaf extracts of *Typha* *angustifolia*, jasmonate, ascorbic acid, nicotinamide, UV-C irradiation, $CaCl_2$, dH_2O, seawater with 9.00 dS m^{-1}, sodium nitroprusside, and $CaSO_4$) improved K^+, Ca^{2+}, and the ratios of K^+:Na^+ and Ca^{2+}:Na^+, while it reduced Na^+ in wheat (*Triticum aestivum*) (Afzal et al. 2008; Maswada and Abd El-Kader 2016; Tabassum et al. 2017), barley (*Hordeum vulgare*) (Anwar et al. 2011; Tabassum et al. 2018), rice (*Oryza sativa* L.) (Imran et al. 2016), sorghum (*Sorghum bicolor*) (Oliveira et al. 2011), dill (*Anethum graveolens* L.) (Ghassemi-Golezani and Nikpour-Rashidabad 2017), safflower (*Carthamus tinctorius*) (Alasvandyari et al. 2017), common bean (*Phaseolus vulgaris*) (Gulmezoglu et al. 2016), pea (*Pisum sativum* L.) (Ghezal et al. 2016), okra (*Hibiscus esculentus*) (Azooz et al. 2015), faba bean (*Vicia faba* L.) (Azooz et al. 2013), lettuce (*Lactuca sativa*) (Ouhibi et al. 2014), and melon (*Cucumis melo*) (Sivritepe et al. 2005). More details about the materials used for priming and their concentrations are shown in Table 1.

Seed priming has been shown to be capable of promoting plant growth under salinity stress through increased nutrient uptake of K^+, Ca^{2+}, and Mg^{2+} while lower uptake of Na^+ and Cl^- which could be considered as one of the seed priming approaches to mitigate salt stress (Afzal et al. 2008; Iqbal and Ashraf 2010; Anwar et al. 2011; Demirkaya 2014; Azooz et al. 2015). This could make seed priming useful to alleviate the plant's salinity stress. Seed priming also participates with important function in regulating the ion transportation and membrane proteins, which manage plant ion homeostasis. For example, Yang et al. (2017) reported little Na^+ and elevated K^+ in quinoa plants grown under 400 mM NaCl stress primed with concentrations of 0.5, 2, 5, 10, 15, 25, and 35% saponin. In rice, 24-h seed priming with 10 ppm of apigenin reduced Na^+ concentration in salt-stressed plants and helped maintain a superior K^+:Na^+ ratio in all plant parts compared to control plants, possibly by adjusting the appearance of confident central Na^+ transporter encoding genes (Mekawy et al. 2018). Iqbal and Ashraf (2010) compared two salt-sensitive and salt-tolerant *Triticum aestivum* cultivars after priming their seeds with chilling at 3 °C for 2 weeks and distilled water hydropriming for 12 h at 22 ± 3 °C. They assigned the increased growth and yield to enhanced concentration of K^+ and Ca^{2+} in the roots and decreased Na^+ in wheat cultivars (Iqbal and Ashraf 2010). A schematic diagram describing the chain reaction following the seed priming is shown in Fig. 2. The diagram illustrates the possible impact of the seed priming on different physiological processes, enhancing tolerance level and final yield.

4.3 Induced Salt Tolerance by Seed Priming Through Osmolyte Organic Solutes

In order to combat stress, plant metabolism is altered in many respects by integrating compatible solute manufacturing to set proteins and cellular structures and/or retain cell turgor through osmotic adjustment and polymerization metabolism to eradicate ROS surpluses and resume the cellular redox equilibrium (Janska et al. 2010; Krasensky and Jonak 2012). Organic plant osmolytes are compounds of low molecular weight, methylated tertiary N and amino acids, and other metabolites of low molecular weight (Chen and Jiang 2010). Osmolytes have unique responses that can defend plant cells other than osmotically (Yancey 2005). Plant performance was also enhanced by the use of exogenous osmolytes under salt stress. A well-recognized adaptive mechanism in salt-stressed plants is the accumulation of osmolytes consisting of proline, glycine betaine, and sugar (Parida and Das 2005; Ashraf and Foolad 2007).

In many crop plants, e.g., safflower (*Carthamus tinctorius*), wheat (*Triticum aestivum*), sorghum (*Sorghum bicolor*), faba bean (*Vicia faba*), lupine (*Lupinus termis*), and common bean (*Phaseolus vulgaris*), and in reaction to salt stress, soluble sugars, free amino acids, proline, and glycine betaine build up (El-Lethy et al. 2013; Semida et al. 2014; Bargaz et al. 2016; Orabi and Abdelhamid 2016; Alasvandyari et al. 2017). The increment in accumulation of these organic osmolytes corresponded with a rise in the rate of salinity (Bargaz et al. 2016). Tolerant genotypes accumulated in some species more proline than susceptible one in reaction to salt stress, e.g., common bean salt-tolerant genotype RIL115 accumulated significant higher proline than the salt-susceptible RIL147 genotype (Bargaz et al. 2016), and in faba bean, the salt-tolerant cultivar Giza 843 had higher proline more than susceptible salt tolerance Giza 3 cultivar (Orabi and Abdelhamid 2016), while in wheat, salt-tolerant cultivar Sakha 93 accumulated significantly more soluble sugars than the salt-susceptible Gemiza 9 cultivar (El-Lethy et al. 2013). In addition, genotype 115 salt-tolerant faba beans appear to be associated with its capacity to accumulate more osmotic solutes than susceptible one (Azooz 2009). Proline therefore prevents crops from salt stress injury by keeping osmoregulation. Furthermore, the roles of proline as an osmolyte or osmoprotective compatible and its antioxidant characteristics to decrease ROS have become a strong plant safeguard against negative abiotic stress, including salt stress (Matysik et al. 2002).

Therefore, as discussed above, a plant under salt stress with greater compatible solute, e.g., glycine betaine, amino acids, soluble sugars, and proline, could be considered salt tolerant. In this regard, several authors reported that seed priming techniques with different materials, e.g., dH_2O, $CaCl_2$, PEG-6000, glycinebetaine, ZnO nanoparticles, gibberellic acid, triacontanol, vitamin B12, aqueous leaf extracts of *Typha angustifolia*, β-amino butyric acid, NaCl, jasmonate, menadione sodium bisulfite, soluble sugars, salicylic acid, glycine betaine, amino acids, and proline, in many crops i.e., in *barley* (Anwar et al. 2011), sorghum (Oliveira et al. 2011), safflower (Alasvandyari et al. 2017), lupine (Ghassemi-Golezani and Nikpour-Rashidabad 2017), cucumber (Sarwar et al. 2017), common bean (Keshavarza and Moghadam 2017), pea (Ghezal et al. 2016), mung bean (Jisha and Puthur 2016), okra (Azooz et al. 2015), *Arabidopsis* (Jiménez-Arias et al. 2015), and wheat (Tabassum et al. 2017). More details about the materials used for priming and their concentrations are shown in Table 1.

On the other hand, exogenous application of compatible solute might not only raise their levels but also protects components of cells, thus raising cellular osmotic pressure. Exogenous amino acids enhanced free amino acids, proline, and soluble sugars in salt-stressed faba bean (Sadak and Abdelhamid 2015). Furthermore, exogenous 5.0 mM proline applications increased proline in common bean plants in saline soil (Abdelhamid et al. 2013a). Exogenous use of glycinebetaine has been reported to improve CO_2 assimilation, decrease stomatal conductance, and improve the efficiency of PS II in maize salt stress plants (Yang et al. 2005). Glycinebetaine functions an important job in protecting plant against salt stress (Ashraf and Foolad 2007) through protein and RuBisCO stabilization (Mäkelä et al. 2000), photosynthetic device protection (Cha-Um and Kirdmanee 2010), osmotic adjustment (Gadallah 1999), and ROS reduction (Ashraf and Foolad 2007). A schematic diagram describing the chain reaction following the seed priming is shown in Fig. 2. The diagram illustrates the effects of seed priming on different physiological processes, enhancing tolerance level and final yield.

Seed priming in 0, 10, 30, and 60 mM glycinebetaine increased salt tolerance in safflower, mainly linked with enhanced CAT and SOD enzyme activity, and protects cell membranes as a consequence of decreased lipid peroxidation and enhanced ion homeostasis (Alasvandyari et al. 2017). Tabassum et al. (2017) reported increased leaf proline and glycinebetaine, and this increase was positively correlated with increases in leaf area, water content, and grain yield while negatively associated with decreases in MDA and Na^+ content when wheat primed with dH_2O and $CaCl_2$. The increased activity of POD and APX antioxidant enzymes with greater amount of osmoprotectants (soluble sugars, soluble proteins, and proline) resulted in protecting okra plants from oxidative injury induced by NaCl stress owing to 50 μM jasmonate seed priming (Azooz et al. 2015).

4.4 Induced Salt Tolerance by Seed Priming Through Antioxidant Defense Response

Salinity causes cell-level oxidative damage in plants. The oxidative burst findings since the molecule of oxygen (O_2) occurs under stress circumstances as an electron acceptor, leading in the building up of reactive oxygen species (ROS) in subcellular compartments, especially in mitochondria and chloroplast. ROS contains superoxide radical ($O_2^{\bullet-}$), singlet oxygen ($^1O_2$), hydroxyl radical ($^{\bullet}OH$), and hydrogen peroxide (H_2O_2). These are oxidizing compounds that can cause injury to DNA, proteins, and lipids (Quiles and López 2004).

Most plant antioxidant studies show that plant production of antioxidants increases in response to salinity to counteract high levels of salt-induced ROS in cells. However, plants with elevated activities of antioxidants can scavenge/detoxify ROS and thus lead to higher salt tolerance (Wise and Naylor 1987; Garratt et al. 2002). Some of the antioxidant enzymes are directly engaged in salt-induced ROS detoxification, i.e., glutathione reductase (GR), superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), and ascorbate peroxidase (APX). Ascorbate, glutathione, and flavonoid are the main nonenzymatic antioxidants engaged in ROS detoxification by salinity (Van Oosten et al. 2013; Begara-Morales et al. 2014).

Significant differences in antioxidant expression for both enzymatic and nonenzymatic are apparent at interspecific or intraspecific concentrations in reaction to salt stress and may rely on germplasms, species, geographic distribution, climate variables, and seasons. For example, plants vary in antioxidant activity under salt environment, and this difference can be assigned to genotypic diversity and the degree of stomata closure that alters the CO_2 fixation rate and avoids photoinhibition (Munns and Tester 2008). While determining if guaiacol peroxidase (POX), the SOD and CAT operate an important function in protecting and recovering cowpea from oxidative salt stress (Cavalcanti et al. 2004). It was reported, however, that the principal antioxidant mechanism, which includes CAT, SOD, and POX, in cowpea mature leaves did not interfere with salt-stressed plants' survival (Cavalcanti et al. 2004).

Many studies confirm the positive association between elevated antioxidant activity and the salt tolerance grade in diverse plant species, even though in some other instances, this is not always right. For instance, the activity of PPO, POX, SOD, CAT, and APX antioxidant enzymes improved with higher concentrations of faba bean salt-stressed plants (Sadak and Abdelhamid 2015). Orabi and Abdelhamid (2016) recorded enhanced activity of antioxidant enzymes POX, CAT, SOD, and PAL in two faba bean cultivars under salt stress, and the greater activity was observed in Giza 843 salt-tolerant cultivar compared to Giza 3 susceptible one.

As discussed above that a plant under salt stress with greater antioxidants, both enzymatic and nonenzymatic could be considered a tolerant one. In this regard, several authors reported that seed priming techniques (e.g., vitamin B12; glycinebetaine; jasmonate; sodium nitroprusside; KCl; $CaCl_2$; jasmonate; glycine betaine; ZNPs; chilling at 3 °C) increased antioxidants in many crops, e.g., wheat, broad bean, lupine, and safflower (Azooz 2009; Islam et al. 2015; Abdel Latef et al. 2017; Alasvandyari et al. 2017). More details about the materials used for priming and their concentrations are shown in Table 1. A schematic diagram describing the chain reaction following the seed priming is shown in Fig. 2. The diagram illustrates the effects of seed priming on different physiological functions, enhancing tolerance level and increased final yield.

The PEG-6000 solution used for seed priming with an osmotic potential of −0.86 Mpa increased CAT and POX activity, and these enzymes can protect sorghum seedlings from oxidative damage in nutrient solutions due to accelerated seed aging and salinity (Oliveira et al. 2012). In latest research by Mekawy et al. (2018), when rice seeds were submerged in a 10 ppm apigenin solution, apigenin pretreatment was connected with the induction of the antioxidant rice protection mechanism by increasing antioxidant CAT and APX activity in the roots, in addition to enhanced accumulation of nonenzymatic antioxidant carotenoids and flavonoids in the shoots, so apigenin pretreatment may reduce the damaging impacts of salinity on rice seedlings by probably triggering induction of antioxidant defense mechanism. Furthermore, Alasvandyari et al. (2017) found that priming with 60 mM glycinebetaine increased salt tolerance in the safflower, mainly owing to enhanced activity of CAT and SOD and decreased cell membrane damage due to decreased lipid peroxidation and enhanced ion homeostasis. Seed priming with ZNPs generally stimulate stressed plant growth, accompanied by increased ascorbic acid and Zn, plus enhanced activity of SOD, CAT, POD, and APX enzymes. Priming with ZNPs in stressed crops led to a decrease in MDA and Na^+ content. These results therefore indicate that seed priming with ZNPs, especially 60 mg L^{-1} ZnO, is an effective method that can be utilized to enhance salt tolerance of lupine plants (Abdel Latef et al. 2017). Improved SOD, APX, and POX activity through seed priming (i.e., vitamin B12; glycine betaine; jasmonate; sodium nitroprusside; KCl; $CaCl_2$) reduced levels of H_2O_2 and MDA in plants under salt stress (Azooz et al. 2015; Islam et al. 2015; Ali et al. 2017; Alasvandyari et al. 2017; Keshavarza and Moghadam 2017). Seed priming with jasmonate, glycinebetaine, ZNPs, and 3 °C chilling increased activity of SOD, APX, and POX which was associated with increased nutrient content of K^+, Ca^{2+}, Mg^{2+}, Ca^{2+}, and Zn in salt-stressed plants (Iqbal and Ashraf 2010; Azooz et al. 2015; Abdel Latef et al. 2017; Alasvandyari et al. 2017). Enhanced SOD, APX, and POX activities were associated with increased organic solutes of proline, free amino acids, soluble sugar, and soluble protein, in salt-stressed plants by seed priming application, i.e., vitamin B12, ZNPs, gibberellins, and salicylic acid (Abdel Latef et al. 2017; Ghassemi-Golezani and Nikpour-Rashidabad 2017; Keshavarza and Moghadam 2017). Moreover, Azooz (2009) reported that *Vicia faba* genotype 115 had a higher accumulation of CAT, POD, APX, and GR antioxidant enzyme activity than genotype 125, when grown in salt with 0 or 140 mM NaCl and seed priming with 0.2 mM salicylic acid; thus they concluded that the salt tolerance genotype 115 appears to be associated with increased antioxidant enzyme activity.

5 Concluding Remarks and Future Perspectives

In conclusion, salt stress is a condition shown in Fig. 1 where too many salts in the soil solution bring about plant growth inhibition or plant death. Salt stress presents a growing threat to plant farming. In order to regulate themselves under saline conditions, plants build up many physiological and biochemical adaptations. Seed priming is a technique that might advance seed performance under salt stress. Seed priming could build up various tolerance mechanisms in seeds against salt stress, for example, variation in photosynthetic pigment, osmotic adjustment, ionic balance, and ion exclusion and antioxidant protection system. A schematic diagram describing the chain reaction following the seed priming is shown in Fig. 2. The diagram illustrates the possible impact of the seed priming on different physiological processes, enhancing tolerance level and final yield. The up-to-date knowledge on seed priming management used in a variety of crops under saline condition is summarized in Table 1. The use of Chemopriming to boost plant tolerance against salt stress is highly promising. Because only limited useful information is available for a large number of plant species, further research is needed to study appropriate substances with precise concentration of priming agents that can guarantee successful seed germination and growth of plant seedling in saline environments. Future research should also focus on molecular, physiological, and metabolic changes caused by salt stress priming mediators. Moreover, further research in the directions proposed in this chapter would be a great extent support for establishment of this know-how in plant management under salt stress in the near future.

Acknowledgments The first author, Dr. Magdi Abdelhamid, would like to express his gratitude to his colleagues at the Department of Botany, National Research Center, Giza, Egypt, for their important contribution to this study in some phases.

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