Stimulating Plant Tolerance Against Abiotic Stress Through Seed Priming

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Abstract

The seed priming process is a physiological method that involves seed hydration (usually within 10–20% of full imbibition) and effective enough for enhancement of seed germination, early seedling growth, and yield under stressed and non-stressed conditions but insufficient to allow radicle protrusion. Primed seeds germinate faster and more uniformly than the non-primed ones. Seed priming is influenced by many factors such as aeration, light, temperature, time, and seed quality and induced a set of biochemical changes in the seed which are required for initiating the germination process. These changes include activation of enzymes, breaking dormancy, metabolism of germination inhibitors, and imbibition. The positive effects of priming on the germination performance of many species are attributed to the induction of biochemical mechanisms of cell repair: the resumption of metabolic activity can restore cellular integrity, through the synthesis of nucleic acids (DNA and RNA) and proteins and the improvement of the antioxidant defense system. Several methods of seed priming were successfully used in agriculture for seed conditioning to accelerate the germination rate and improve the seedling uniformity such as seed priming with water (hydropriming), plant growth regulators, beta-aminobutyric acid, 5-aminolevulinic acid, osmoprotectant, melatonin, chitosan, plant extract, polyethylene glycol, and inorganic salts. It is worthy to mention that all these methods showed pronounced effect on germination, seedling growth, and yield of different crops under normal or stress conditions.

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10.1   Introduction

In nature, plants often face the challenge of severe environmental conditions, which include various biotic and abiotic stresses that exert adverse effects on plant growth and development causing considerable losses in the crop productivity. Plants are subjected to a variety of abiotic stress such as salinity, drought, high temperature, low temperature, etc. that reduced germination rate and seedling growth with significant variations from crop to crop (Hamidi and Safarnejad 2010). Abiotic stress causes many physiological and biochemical changes in the seedlings, which include the generation of reactive oxygen species (ROS), leading to membrane damage and cell leakage and destruction of photosynthetic components (Jisha and Puthur 2014). ROS are known to exacerbate imbalance between light absorption and its utilization by inhibiting Calvin-Benson cycle activity (Logan et al. 2006). ROS also reduce content and activity of ribulose bisphosphate carboxylase oxygenase (RUBISCO) enzyme which leads to higher electron flux to O_2 coupled with reduced CO_2 accumulation (Zhou et al. 2006; Ahmad et al. 2015), and they can be extremely reactive with several cellular constituents such as proteins, lipids, and nucleic acids (Hasanuzzaman et al. 2013), which in turn results in negative effects on metabolism and cellular structures (França et al. 2007; Mouradi et al. 2016). Free radical oxidations and protein enzymatic dehydrogenation and aldehyde oxidation might contribute to seed quality reduction (Ghassemi-Golezani et al. 2010).

In many plants, germination, seedling growth, and subsequent crop yield can be inhibited by salinity stress (Soccio et al. 2010; Carvalho et al. 2011). *Salinity* has an adverse effect on seed germination and seedling growth of several crops either by creating an osmotic potential in the rhizosphere of the plant that inhibits the absorption of water or creates toxic effect to the roots and whole crop because of Na^+ and Cl^- (Khajeh-Hosseini et al. 2003; Munns and Tester 2008). Moreover, salinity has a negative effect on plasma membrane by affecting on its permeability which in turn modulates the pattern of ion leakage (Sairam et al. 2002). Salt tolerance of plants can be increased by treatment of seeds with NaCl solution prior to sowing (Sivritepe et al. 2003). Farhoudi et al. (2007) reported that priming of canola seed decreased the absorption of harmful ion and cell damage of canola seedling under salinity stress.

Drought is one of the most important environmental factors limiting plant growth and productivity. Soltani et al. (2008) mentioned that as the drought severity increased, the germination rate linearly decreased in unprimed cotton seeds, but primed seeds had lower reduction slope. Moreover, Khatami et al. (2015) stated that some priming treatments were sufficient to invigorate the corn seed germination under drought stress, since hormone priming under moderate drought and osmopriming under severe drought were the best methods for seed improvement.

Low-temperature conditions decreased plant growth rate because of inhibition of photosynthesis and increasing photooxidative injury of the photosystems. Photooxidative damage caused lipid peroxidation and degradation of chlorophyll and carotene. Plants exert many physiological and biochemical changes under low-temperature conditions that make them survive under these

conditions (Xin and Browse 2000). In general, physiological and biochemical dysfunctions induced by low temperature in plants are not equal and most of them can be convert if plant return to optimum condition before appearance of damage, since disturbances of physiological and biochemical functions are reversible.

Heat stress is often defined as the rise in temperature beyond a threshold level for a period of time sufficient to cause irreversible damage to plant growth and development. In general, a transient elevation in temperature, usually 10–15 °C above ambient, is considered heat shock or heat stress. However, heat stress is a complex function of intensity (temperature in degrees), duration, and rate of increase in temperature. The extent to which it occurs in specific climatic zones depends on the probability and period of high temperatures occurring during the day and/or the night (Wahid et al. 2007a).

The time from sowing to plant establishment is a crucial period in crop growth (Bray 1995), with a direct impact on final yield and quality (Gupta et al. 2008) especially under abiotic stress. So, several ways for enhancing the plant tolerance toward abiotic stress have been experimented like breeding of plants and developing transgenics (Jisha et al. 2013). Moreover, some studies on different plants showed that seed priming treatments have effectively increased germination and seedling growth either at normal conditions or stressed conditions (Bradford 1986). Since, efficient seed germination, rapid and uniform seedlings emergence lead to successful culture establishment (Chen and Arora 2011).

10.2   Seed Priming

Seed priming is a simple, safe, economic, and effective approach for enhancement of seed germination, early seedling growth, and yield under stressed and non-stressed conditions (Sedghi et al. 2010). Seed priming is a form of seed preparation in which seeds are presoaked before planting with a certain solution that allows partial hydration but not germination and redried to original moisture content (Ahmad et al. 2012). The seed priming process is a physiological method that involves seed hydration (usually within 10–20% of full imbibition) (Pill 1995), sufficient to permit pre-germinative metabolic events to proceed, but insufficient to allow radicle protrusion (Bradford 1986). Primed seeds germinate faster and more uniformly than the non-primed ones.

During priming, the germination process is not completed, but metabolic activities for radical protrusion may be initiated (Heydecker et al. 1973). At the cellular level, few processes have been described to act during priming, some of these being activation of cell cycle (De Castro et al. 2000) and mobilization of storage proteins (Gallardo et al. 2001). The priming process induces the rate of seed germination and is associated with the initiation of germination-related processes (Soeda et al. 2005) and repair processes (Sivritepe and Dourado 1995) and increases various free radical-scavenging enzymes, such as superoxide dismutase, catalase, and peroxidase (Gallardo et al. 2001).

Several seed priming methods were successfully used in agriculture for seed conditioning to accelerate the germination rate and improve the seedling uniformity (Nouman et al. 2012; Aghbolaghi and Sedghi 2014; Bagheri 2014; Lara et al. 2014). Moreover, seed priming helps many crops to neutralize the adverse effects of abiotic stress (Ashraf and Foolad 2005; Zhang et al. 2012; Hameed et al. 2013; Jisha et al. 2013; Jisha and Puthur 2016).

10.2.1 There are Three Principal Methods of Seed Priming

1. *Hydropriming (water-only treatments)*: soaking of seeds with water overnight and then drying before sowing markedly improve plant stand, establishment, vigor, and the final yield (Harris et al. 1999). Seeds are submerged in water with or without aeration. Therefore, water is freely available to seeds, its uptake only being governed by the affinity of the seed tissue for water (Taylor et al. 1998). As a main drawback, seed germination can proceed until radicle protrusion. Thus, the process needs to be stopped at a precise moment, before phase III begins. Another disadvantage is that seeds are not equally hydrated, which results in a nonuniform activation of the physiological processes necessary to synchronize and improve germination (McDonald 2000).
2. *Solid matrix priming or matri-priming*: hydrated solid matrices soaked with osmotic solutions (McDonald 2000), such as hydrated sand (Hu et al. 2005), peat, and vermiculite (Taylor et al. 1998), or cotton soaked with osmotic solutions; involves the use of a wet organic or inorganic material (Parera and Cantliffe 1994), which simulates the natural imbibition processes taking place in the soil (McDonald 2000). The substrate must possess the given characteristics: low matric potential, high seed safety, high specific surface (i.e., high surface to volume ratio), negligible water solubility, high adhesiveness to seed surface, and high capacity to retain water (Khan 1991).
3. *Osmotic priming (osmopriming)*: osmopriming is the process that involves the use of osmotic solutions with a low water potential to control seed water uptake. The most common substances used for osmopriming are polyethylene glycol (PEG), inorganic salts, mannitol, glycerol, and plant hormones (Taylor et al. 1998; Foti et al. 2002; Tiryaki and Buyukcingil 2009; Afzal et al. 2013; Farooq et al. 2015).

The three methods may be grouped into two categories: non-controlled water uptake (hydropriming) and controlled water uptake (osmopriming and solid matrix priming) (Taylor et al. 1998).

Bio-priming: Additional method includes seed coating with bacteria (bio-priming or bio-osmopriming), e.g., *Trichoderma* spp. (Pill et al. 2009; Begum et al. 2010) and *Pseudomonas aureofaciens* (Warren and Bennett 1999). Bio-priming has been able to control damping-off of seedlings in sweet corn (*Zea mays* L.) (Callan et al. 1990),

cucumber (*Cucumis melo* L.) (Pill et al. 2009), pea (*Pisum sativum* L.), and soybean (*Glycine max* (L.) Merr.) (Taylor et al. 1994).

10.2.2 Factors Affecting Seed Priming Process

Seed priming is influenced by many factors such as aeration, light, temperature, time, and seed quality.

1. *Aeration* is considered an important step to assist seed respiration (Bujalski and Nienow 1991) and seed viability and contributes to synchronize the emergence (Heydecker et al. 1975) and ensures a safer seed habitat. However, the effect of aeration varies according to species: in onion, aeration of the PEG solution increased the germination percentage, compared to non-aerated treatment (Heydecker and Coolbear 1977; Bujalski et al. 1989). By contrast, no difference was observed in the germination of lettuce between aerated and non-aerated K_3PO_4 priming (Cantliffe 1981).
2. *Light* effect is widely varied according to species. Khan et al. (1978) mentioned that illumination during priming of celery seeds may reduce dormancy. On the other hand, the best results with lettuce were obtained with priming in the dark (Cantliffe et al. 1981).
3. *Temperature* is another important variable, as it affects the speed of chemical reactions. Treatment temperature varied between 15 (several cases) and 30 °C (rice in hydropriming, Basra et al. 2005). Temperatures of about 15 °C during priming were shown to improve the overall seed performance in most species (Bradford 1986), whereas lower temperatures slowed the germination processes, requiring longer times to achieve the same results (McDonald 2000). The range of temperatures normally used in priming varies between 15 and 20 °C.
4. *Treatment duration* is widely varied according to species and experiment, from a minimum of 8 h (sunflower primed in a salt solution, Wahid et al. 2008) to a maximum of 14 days (four ornamental species, Finch-Savage et al. 1991). Treatment duration mainly depends on the type of osmotic solution, osmotic potential, temperature, and crop species. It also depends on the specific time and likelihood of radicle protrusion: long priming can more easily lead to this occurrence, creating irreversible damage during drying-back (Parera and Cantliffe 1994).
5. *Seed quality* is a key aspect influencing the effects of priming. A vigorous seed, free from pathogens is an essential requisite for a good priming result (Cantliffe et al. 1987), in contrast to the belief that this technique may improve the performance of seeds of intrinsic modest quality. Other seed characteristics may influence priming process. For instance, osmopriming with PEG solution is not suitable for seed treatment of sorghum with high content of tannin, because tannins can be removed with the solution treatment and determine a reduction of germination (Patanè et al. 2008). In fact, tannins reduce seed susceptibility to insects, birds, and mold diseases and protect from weathering (Beta et al. 1999).

In this specific case, it is advisable to adopt treatment solutions different from PEG or others technique, such as bio-priming (Patanè et al. 2008). Moreover, Bradford (1986) mentioned that composition of solution and osmotic potential had pronounced effect on seed priming.

10.3 Triphasic Model of Seed Imbibition

In orthodox seeds the dry seed, ready for germination, exhibits a triphasic pattern of water uptake (Bewley and Black 1978). *Phase I* is the rapid water uptake that is largely a consequence of the matric forces exerted by the seed. During this phase, DNA and mitochondria are repaired and proteins are synthesized using existing messenger ribonucleic acid (mRNA) (McDonald 2000). *Phase II* is a lag phase, in which seed water potential is in balance with that of the environment. In this phase the major metabolic changes preparing the embryo for germination occur, including the synthesis of mitochondria and proteins by new mRNA. Thus, phase II is also called activation phase. *Phase III* is a second rapid uptake of water occurs and the radicle emerges so called visible germination (Bewley and Black 1978; Bradford 1995). Phases I and II represent the most delicate phases for the process of germination and are crucial for a successful seed priming (Bewley 1997). The triphasic model has deep implications for seed viability. The seed tolerates a return to the initial moisture necessary for storage, a process known as drying-back or redrying, when it is in phase I or II, whereas phase III is too advanced to allow a drying-back without seed damage (Taylor et al. 1998). According to the triphasic model, the start of germination is associated with a rapid synthesis of RNA and proteins, to carry out the repairing processes before the beginning of DNA replication (Osborne 1983). Seed priming typically involves an extension of phase II, which in turn permits the completion of more repair processes (Bray 1995), and allows the drying-back, which is necessary when the final sowing is postponed (industrial seed production). The postponement of phase III involved in priming plus redrying results in a better seed performance under favorable conditions.

10.4 Biochemical Changes Induced by Priming

Seed priming induced a set of biochemical changes in the seed which are required for initiating the germination process. These changes include activation of enzymes, breaking dormancy, metabolism of germination inhibitors, and imbibition to start the germination process (Ajouri et al. 2004; Farooq et al. 2010). Some or all of these changes that precede germination are triggered by seed priming and persist following the redrying of seeds (Asgedom and Becker 2001). Thus, upon sowing, primed seed can rapidly imbibe and revive the seed metabolism, resulting in higher germination percentage (Rowse 1995). Moreover, seed priming may repair some damage in the membrane caused by deterioration and result in better germination pattern and higher vigor level compared with non-primed seeds (Ruan and Xue 2002).

Priming showed stimulatory effects in the early stages of germination by mediation of cell division in germinating seeds (Hassanpouraghdam et al. 2009). The increase in speed of germination and germination percentage may be due to the modification of physiological and biochemical nature of seed embryo and its associated structures, i.e., pre-enlargement of the embryo (Austin et al. 1969), and biochemical changes like enzyme activation; gibberellin-like substances may be released during phase II of germination which triggers the synthesis of hydrolytic enzymes that causes the early availability of high-energy compounds (Basra et al. 2005) and vital biomolecules to the germinating seedling (Renugadevi and Vijayageetha 2006).

The positive effects of priming on the germination performance of many species are attributed to the induction of biochemical mechanisms of cell repair: the resumption of metabolic activity can restore cellular integrity, through the synthesis of nucleic acids (DNA and RNA) and proteins and the improvement of the antioxidant defense system (Bewley and Black 1994; Di Girolamo and Barbanti 2012).

10.4.1 Effects on DNA

A strong increase in DNA synthesis occurs at the end of germination (phase III) in both primed and unprimed wheat grains, as shown by Dell'Aquila and Taranto (1986). Thereafter, an increase in DNA was observed 14 days after the seed priming, when the seed had entered the irreversible germination phase (Bray 1995). The positive effects of priming on DNA are offered by a study on *Brassica oleracea* L., where an aerated hydration determined an advance in DNA synthesis (Thornton et al. 1993). In spite of its crucial role, the amount of DNA which is needed in the repair processes is only 20–30% of the total DNA synthesized during priming. The rest is mainly represented by mitochondrial DNA; in fact, the number of mitochondria was shown to rapidly increase during priming in leek seeds (Ashraf and Bray 1993). The enhancement of DNA replication during priming depends on species, cultivar, seed lot quality (Lantieri et al. 1994), and treatment conditions (Ozbingol et al. 1999).

10.4.2 Effects on RNA

Priming allows the recovery of rRNA integrity (Coolbear et al. 1990), in turn ensuring a correct coding of amino acids for the synthesis of proteins during seed germination. Bray et al. (1989) proved that this accumulation involved rRNA (ribosomal RNA, 85% of total RNA) in a turnover between degradation of damaged rRNA and synthesis of new rRNA, while the level of mRNA (messenger RNA, 0.5% of total RNA) remained constant. rRNA is as much necessary to repair cell damages as DNA.

10.4.3 Effects on Protein Synthesis

Protein synthesis is an essential requisite for germination and starts after few minutes from hydration (Cheung et al. 1979). Bray (1995) showed that the amount of synthesized protein observed 2 days after germination in primed leek seed was the same as that observed 4 days after germination in unprimed seed. Chen et al. (2012) observed an increase of dehydrin in spinach (*Spinacia oleracea* L.) during osmopriming. This increase was also observed during germination of primed seeds in chilling stress and desiccation stress, suggesting that osmopriming may play a positive role in the tolerance to these stresses.

10.4.4 Effects on Enzymes

Osmopriming induce the synthesis and activation of enzymes catalyzing the breakdown and mobilization of reserve substances (Varier et al. 2010). Sung and Chang (1993) mentioned that enzymes responsible for the mobilization of reserve carbohydrates (α- and β-amylases) and lipids (isocitrate lyase) are activated due to priming process. This effect is associated with the water deficit induced by osmopriming, which is supposed to determine a mobilization of reserve proteins (Varier et al. 2010).

In fact, priming appears to strengthen defense system (antioxidant enzymes): seed priming was associated with an increase in CAT expression in *Arabidopsis* (Gallardo et al. 2001) and sunflower (*Helianthus annuus* L.) (Kibinza et al. 2011) and maize seeds (Chiu et al. 2002). In sunflower seeds, Bailly et al. (1998, 2000) showed that osmopriming with PEG led to an increase of SOD and CAT, in response to the rise of metabolic activity during priming, which is responsible for a secondary production of AOS from mitochondrial respiration and/or lipid peroxidation. It appears, therefore, that the defense system of the antioxidant enzymes is enhanced in response to a higher amount of potential threats.

Several methods of seed priming were successfully used in agriculture for seed conditioning to accelerate the germination rate and improve the seedling uniformity as seed priming with water, plant growth regulators, beta-aminobutyric acid, 5-aminolevulinic acid, osmoprotectant, melatonin, chitosan, plant extract, polyethylene glycol, and inorganic salts. It is worthy to mention that all these methods showed pronounced effect on germination, seedling growth, and yield of different crops under normal conditions or stressful conditions.

10.5 Seed Priming with Water (Hydropriming)

Soaking seeds with water overnight and then drying before sowing markedly improved seedling emergence, plant growth, establishment, vigor, and the final yield as reported by Harris et al. (1999) and Ahmad and Shad (2010). On the other hand, Harris et al. (2002) and Basu et al. (2005) reported that effects of

hydropriming persisted only till early vegetative growth of maize. The primed seed germinated soon after planting compared with untreated dry seed, since the early emergence and its effect on early maturity of primed seed may be due to the completion of pre-germinative metabolic activities that making the seed ready for radical protrusion (Rajpar and Wright 2000). Moreover, Rajpar et al. (2006) reported that primed seeds overnight took significantly fewer days to emerge and reach maturity when compared to the untreated dry seed, whereas 36 h primed seeds showed poor germination and 48 h primed seeds inhibited germination. This inhibition may be attributed to the long period of priming that led to excess water in the seeds and greater reduction in the O_2 availability to the embryo. This was reported by Perry and Harrison (1974) who stated that excess of water during priming had inhibitory effect on seed germination of *Beta vulgaris*. The reduction in O_2 availability could lead to an inhibition of ethylene synthesis (Beyerjr et al. 1985) and consequently seed germination. Dawood (2005) demonstrated that the changes in the chemical composition and anti-nutritional factors under the effect of soaking of canola seeds with water for 24 h depend on the variety and caused a marked decrease in tannins and glucosinolates, total polyphenols, and phytic acid of canola meal. In this regard, Kibinza et al. (2011) showed that priming of sunflower seeds improves germination percentages due to the significant drop in H_2O_2 accumulation and restoration of catalase activity that protects stressed seeds against damages caused by ROS activities. Moreover, Kester et al. (1997) reported that seed priming is able to increase protein content in plant tissue via conferring protection to the cellular proteins damaged, improving the performance of the protein synthesis system, and also increase in protein L-isoaspartyl methyltransferase enzyme that repairs plant tissue protein.

10.6   Seed Priming with Plant Growth Regulators

Priming seeds with plant growth regulators has been reported to be beneficial to growth stages and yield of some crops and known as a strategy to alleviate the harmful effect of environmental stresses (Bahrani and Pourreza 2012; Jisha et al. 2013). For instance, soaked rye seeds with gibberellic acid increased germination percentage under water stress conditions (Ansari et al. 2013). The germination of pretreated pepper seeds with salicylic acid improved significantly under high salinity levels (Khan et al. 2009). In addition, Nascimento (2004) documented that seed priming with ethylene minimizes the effect of high temperatures on lettuce seed germination. Seed priming with brassinosteroids (BR) increased peroxidase (POD), superoxide dismutase (SOD), and catalase (CAT) activities in *Medicago sativa* seedlings under salinity stress (Zhang et al. 2007). Priming *Vicia faba* seed with salicylic acid improved salinity tolerance due to enhanced activities of CAT, ascorbate peroxidase (APX), POD, and glutathione reductase (GR) (Azooz 2009). Priming seeds of *Agropyron elongatum* with gibberellin (GA) and abscisic acid (ABA) induced CAT and SOD activities under drought conditions when compared to unprimed seeds (Eisvand et al. 2010). Maize seeds primed with hormones exhibited acquired abiotic stress tolerance through a more responsive antioxidative system (Afzal et al. 2008;

Farooq et al. 2008). Moreover, phytohormonal priming can enhance seed germination through enhancing some enzymes such as amylase activities and protease that hydrolyzed starch and protein molecules into simple forms available for the embryo to germinate (Miransari and Smith 2014). Hormonal priming was found also to reduce the reactive oxygen species (ROS) produced under $PbCl_2$ stress, and it can alleviate the stress by controlling the oxidative damage on seed germination and embryo growth under stress conditions (Sajedi et al. 2011). Although hydropriming and hormonal priming on soybean can improve seedling establishment and field performance, hormonal priming using auxin, cytokinin, and GA_3 were the most appropriate priming treatments for soybean seeds grown under Pb stress conditions (Abu-Muriefah 2017). ROS produced under stress conditions often interact with the phytohormone priming, and this interaction between ROS and phytohormone could be antagonistic or synergistic (Golldack et al. 2013).

10.6.1 Auxin

Generally, auxins are the best hormones to use because they are nontoxic to plants over a wide range of concentration and effective in promoting root system of large number of plant species. Auxins might regulate cell elongation, cell division, tissue swelling, formation of adventitious roots, callus initiation, and induction of embryogenesis at very low concentrations (Vanderhoef and Dute 1981). The principal auxin in plants is indole-3-acetic acid (IAA) that produced mainly in the shoot apex bud and young leaves of plants. Other meristematic tissues, flowers, fruits, and young seeds have also been shown to be sites of this hormone production. IAA has wide range of effects on many processes such as cell division, vascular tissue differentiation, root initiation, flowering, fruit setting, ripening, senescence, and gravitropism (MacDonald 1997). Furthermore, IAA stimulated cell elongation and apical dominance (Wang et al. 2001), increased photosynthetic activities (Naeem et al. 2004), and activated the translocation of carbohydrates during their synthesis (Awan et al. 1999).

It is well known that IBA is an auxinic hormone and plays a regulatory role in many vital processes within plants such as growth, development, and vascular and pollen formation. Its function on growth, including embryo development, is controlled by its transport which is regulated by transcriptional factors (Hayashi 2012). Another important function of the IBA is its role in cell elongation in the growing embryo (Hauvermale et al. 2012). Auxin by itself is not a necessary hormone for seed germination (Hentrich et al. 2013); however, according to the analyses regarding the expression of auxin-related genes, auxin is present in the seed radicle tip during and after seed germination.

10.6.2 Cytokinins

It was found that cytokinins are able to stimulate seed germination by alleviating the stresses such as drought, salinity, and heavy metal as well as oxidative stress (Peleg and Blumwald 2011; Miransari and Smith 2014). Cytokinins have the ability to regulate a range of cell activities including cell division and seed germination. Heyl et al. (2012) mentioned that cytokinins were active at all stages of germination and enhance the activity of meristematic cells in epicotyls and hypocotyls. These hormones have potent effects on plant physiology and are intimately involved in the regulation of cell division, apical dominance, chloroplast development, anthocyanin production, and maintenance of the source-sink relationship (Hutchkinson and Kileber 2002). In addition, cytokinins are regarded as the most important senescence-retarding hormones, and their application has been demonstrated to prevent the degradation of chlorophyll and photosynthetic proteins as well as reverse leaf and fruit abscission (Pospíšilová et al. 2000). Kinetin is a synthetic cytokinin known to significantly improve plant growth and development even grown under environmental stress. It stimulates leaf expansion and development of reproductive organs and delays senescence (Shah 2007).

10.6.3 Gibberellins

Gibberellins are diterpenoid, regulating seed germination and plant growth through its antagonistic effects with ABA. Abu-Muriefah (2017) stated that GA_3 priming was found to enhance seed germination, maybe through its effect on stored food within seeds, and makes it available for embryos during germination processes. The endosperm within seeds becomes available to the embryo via the activities of some hydrolase enzymes. It is well known that GA_3 stimulates the synthesis and production of the hydrolases, especially α-amylase, resulting in the germination of seeds. In this regard, Yamaguchi (2008) found that gibberellins were able to induce a range of enzymes necessary for seed germination including amylase, protease, and glucanase. Moreover, seed germination is often controlled through suppression effects of excess ABA on the expansion of embryo organs caused by inhibition of GA_3 effects on the growth of radicle and hypocotyl (Voegele et al. 2011). In addition, gibberellins are essential in seed germination for the production of mannanase that is necessary for seed germination (Wang et al. 2005).

10.6.4 Abscisic Acid (ABA)

ABA inhibited the activity of many enzymes involved in germination of pigeon pea, barley grains, and soybean as reported by Sneideris et al. (2015), Staroske et al. (2016), and Abu-Muriefah (2017), respectively. Although ABA had negative effects on seed germination process, it positively affects seed dormancy and plant activities under biotic and abiotic stresses (Popko et al. 2010). Chiu et al. (2016) stated that

high ABA concentrations can inhibit seed germination in many species probably due to the inhibitory effect of ABA on the activity and/or the synthesis of some enzymes involved in the degradation of endosperm cells such as α-amylase within seeds, which considered an important process for seed germination. Moreover, the inhibition of seed germination at high levels of ABA was through inhibition of the radicle expansion and suppression of some transcriptional factors, which can negatively affect the process of seed germination (Graeber et al. 2010).

10.6.5 Ethylene

Ethylene regulates plant responses under different stress conditions and controls many processes in plants, including seed germination (Keunen et al. 2016) and embryo radicle growth (Baskin et al. 2003). It was found that ethylene concentration increased during seed germination process of many species including wheat, corn, soybean, and rice (Zapata et al. 2004). 1-Aminocyclopropane-1-carboxylic acid (ACC), the precursor of ethylene, can enhance seed radicle emergence through the production of ethylene which is produced in the radicle (De Poel and der Straeten 2014). In this regard, seed priming with ethylene precursor ACC (1-aminocyclopro pane-1-carboxylic acid) increased the rate of germination in lettuce seeds (Nascimento 2004), but it didn't affect significantly the rate of germination in ryegrass (Tiryaki et al. 2004). However, under abiotic stress conditions and GA$_3$-deficient mutants, ethylene can play the same role of GA$_3$; therefore ethylene priming makes seeds able to germinate completely at such conditions (Matilla and Matilla-Vazquez 2008).

10.6.6 Salicylic Acid

Salicylic acid (SA) acts as an endogenic phytohormone from phenolic compounds (among the group of ortho-hydroxyl benzoic acid), having the ability of antioxidant defense system, and regulates various physiological and biochemical processes in plant such as stomata conductivity (Hayat et al. 2010), activity of photosynthesis pigments (Hayat et al. 2005), maintenance of tissue water contents and reduced membrane permeability (Farooq et al. 2008), adjustment of the activity of antioxidant enzymes (Carvalho et al. 2011), and tolerance to environmental stresses (Kabiri et al. 2012). In addition, Sakhabutdinova et al. (2003) reported that salicylic acid treatments maintain IAA and cytokinin levels in the plant tissues, which enhanced the cell division.

Regarding priming process, it was reported that salicylic acid pretreatment produced a higher total biomass and seed vigor index (Kabiri et al. 2012; Sharifzadeh et al. 2013) and increased seedling field emergence because the salicylic acid treatment prevented the decrease in indoleacetic acid and cytokinin content completely which reduces inhibition of plant growth (Afzal et al. 2006; Ansari and Sharifzadeh 2012).

Seed priming with salicylic acid induced salinity tolerance (Kumar et al. 2010; Ahmad et al. 2012, 2015) via increasing SOD activity which quenches oxygen radicals (Gautam and Singh 2009; Orabi et al. 2015) and reducing membrane permeability and leakage of ions like NO_3^- in wheat and canola (Wahid et al. 2007b; Sakr and Arafa 2009) and enhancing chlorophyll contents and sugars which is necessary for osmotic regulations as well as retards ethylene biosynthesis (Hamid et al. 2008). Moreover, Dellali et al. (2012) recognized that salicylic acid priming at the seedling growth stage alleviated salt-induced oxidative stress by reducing malondialdehyde (MDA) and H_2O_2 content.

Furthermore, seed priming with salicylic acid improved chilling tolerance and increased germination (Sedghi et al. 2010), via activation of antioxidants, maintenance of tissue water contents, and reduced membrane permeability (Farooq et al. 2008), as well as protected structure of plant cell (Horvath et al. 2007). Farooq et al. (2008) showed that maize seed priming by salicylic acid solution improved germination characteristics and seedling root and shoot growth under both normal and low temperature conditions through activation of antioxidant enzymes system, including catalase (CAT), superoxide dismutase (SOD), and ascorbate peroxides (APX). Meanwhile, Pouramir-Dashtmian et al. (2014) revealed that seed priming with salicylic acid solution improved rice seedling growth under low temperature condition via increasing proline, soluble sugar, and protein content.

Regarding optimum concentration, it was found that seed priming with either 20 mg L^{-1} acetylsalicylic acid or salicylic acid seems to be the suitable concentration that showed maximum seed invigoration and better performance in maize through inducing SOD activity and improving nutrient contents in root and shoot as reported by Ahmad et al. (2015). In addition, Hayat et al. (2005) reported that soaking of wheat grains with low concentrations of salicylic acid significantly promoted growth of wheat seedlings. Pretreatment of barley seeds with 1150–1252 µmolar salicylic acid significantly increased the number of seed in spike and thousand seed weight and thus enhanced seedling emergence in field condition (Khaliliaqdam and Mir-Mahmoodi 2013.

10.7 Seed Priming with Beta-Aminobutyric Acid (BABA)

Recently, nonprotein amino acids like β-aminobutyric acid (BABA) were employed in seed priming of various crops against biotic and abiotic stress (Worrall et al. 2012). BABA is known as a potent inducer of resistance in plants against nematodes (Oka et al. 1999), microbial pathogens (Cohen 2002), insects (Hodge et al. 2005), and abiotic stress (Jakab et al. 2005; Zimmerli et al. 2008). According to Zhong et al. (2014), BABA can bring plants into a sensitization state in which defenses are not expressed, but are able to react more rapidly and/or more strongly to various stress. BABA-induced priming functions by the interaction with several hormones like salicylic acid (SA), abscisic acid (ABA), and ethylene (Jakab et al. 2005) or by causing a cascade of signaling processes mediated through H_2O_2 (Cohen et al. 2010). Jisha and Puthur (2016) mentioned that priming rice grain with BABA reduced MDA content of seedlings through reducing the lipid peroxidation of

biomembranes and increasing antioxidant enzyme activities and thus improved the PEG-6000 and NaCl stress tolerance of rice seedlings.

10.8   Seed Priming with 5-Aminolevulinic Acid (ALA)

5-Aminolevulinic acid (ALA) is an aliphatic precursor in the biosynthesis of all porphyrin compounds such as chlorophyll and heme (Wang et al. 2004). ALA is a biodegradable herbicide and insecticide, but it has promotional effects on the growth and photosynthesis of crops and vegetables and is harmless to humans, animals, and crops (Hotta et al. 1997a, b). Rae-hyun and Song (2007) demonstrated that the application of *Rhodopseudomonas* sp. which produced indole-3-acetic acid and 5-aminolevulinic acid could increase the germination percentage of tomato seed by 30.2%. ALA is able not only to act as an antioxidant enzyme promoter but also to stimulate nitrate reductase activity (Beyzaei et al. 2014) and the respiration rate and ATP synthesis (Fu et al. 2014). ALA not only promotes the growth and yield of crop plants but also acts as an alleviator of oxidative damage and enhances the activity of antioxidant enzymes such as superoxide dismutase (SOD), peroxidase (POD), and ascorbate peroxidase (APX) to encounter radicals under stress conditions, i.e., drought stress and salinity stress (Li et al. 2011; Liu et al. 2011; Zhang et al. 2013a). Korkmaz et al. (2010) reported that seed soaking with 25 ppm ALA enhanced the germination rate and seedling uniformity, thereby providing chilling stress tolerance of pepper seedling. Kanto et al. (2015) suggested that rice seed priming with ALA at 0.5 μg mL^{-1} could ameliorate the germination capacity even after exposure to the accelerated ageing treatment by enhancing the activity of antioxidant enzymes to scavenge ROS during rice seedling growth under accelerated ageing.

10.9   Seed Priming with Osmoprotectants

Many plants tolerate stress by production of different types of organic solutes called osmoprotectants (compatible solutes or osmolytes) which lower the osmotic potential and attract water molecules into the cell and ultimately maintain the cell turgor. These compatible solutes including soluble sugars, sugar alcohols, proline, glycine-betaine, etc. are low molecular weight, highly soluble in water, and nontoxic to plant even at higher cytosolic concentration (Hoque et al. 2007).

Generally, these compatible solutes protect plants from stress injury through different means, including protection of cytoplasm and chloroplasts from Na$^+$ damage and scavenging of reactive oxygen species (Smirnoff and Cumbes 1989), stabilization of proteins and protecting membrane structure (Bohnert and Jensen 1996), maintaining the osmotic balance, and general maintenance of physiological stability of plants under stressful conditions (Farooq et al. 2009).

10.9.1 Glycinebetaine (GB)

Glycinebetaine (GB) is a quaternary ammonium compound, an amino acid derivative, and regarded as one of the most effective compatible solutes that protect plants from injury of abiotic stresses. GB application improves growth, survival, and tolerance of a wide variety of plants under various stress conditions (Ashraf and Foolad 2007) by regulating a number of physiological and biochemical processes (Qureshi et al. 2013), maintaining turgor pressure (Agboma et al. 1997), enhancing net CO_2 assimilation rate (Lopez et al. 2002), protecting the functional proteins and enzymes (e.g., Rubisco) and lipids of the photosynthetic apparatus, and maintaining electron flow through thylakoid membranes (Allakhverdiev et al. 2003) and regulation of photosynthetic machinery and ion homeostasis (Raza et al. 2014). Further, GB induces defense response in crops against reactive oxygen species (ROS) produced due to biotic and abiotic stresses and plays a vital role in the process of osmotic adjustment in many crops under environmental stresses (Gadallah 1999). Moreover, it may act as an antitranspirant which allowed the plant to access more water for a long period and facilitates photosynthesis as reported by Agboma et al. (1997).

The main role of GB in plants exposed to saline soil is considered to be maintaining osmotic regulation in cells (Gadallah 1999). It was suggested that GB supports various transporters for normal functioning under salt stress. From this, it can be proposed that GB has a protective effect in discriminating Na^+ against K^+ under saline states (Mansour 1998). The second possible role of GB is that it might enhance vacuolar efficiency in the roots of salt-stressed plants for accumulating more Na^+ as reported by Rahman et al. (2002). Gadallah (1999) reported that GB improves germination and seedling growth of many crops under stressful condition. Plants treated with GB also maintain higher antioxidative enzyme activities that minimize oxidative stress (Ma et al. 2006). The application of GB has an important role in water availability for the imbibition of germinating seeds during limited water. Under salinity conditions, GB increased seed germination by enhancing the osmotic pressure (Sakamoto and Murata 2000) and alleviated lipid peroxidation and facilitated the protection of membrane functions (Hu et al. 2012), protected the photosynthetic machinery by stabilizing the activity of repair proteins (Murata et al. 2007), and provided a direct protective effect on antioxidant enzyme activities under salinity stress (Hoque et al. 2007).

Cuin and Shabala (2005) suggested that compatible solutes, and GB in particular, regulate the net fluxes of Na^+ and K^+ across the plasma membrane at the cellular level in response to NaCl stress. Priming safflower seeds with GB (60 mM) was the most effective treatment that enhanced the plant's tolerance to salt stress during the germination stage. Dawood and Sadak (2014) mentioned that soaking canola seeds with different concentrations with GB caused significant increases in IAA, proline, and total soluble sugars and significant decreases in MDA, H_2O_2, and antioxidant enzymes (POX, PPO, SOD, CAT, APX, and NR) in canola plants irrigated with different levels of water relative to corresponding controls. All GB treatments caused significant increases in seed yield, oil, carbohydrate, protein, total phenolic content, tannins, and antioxidant activity of the yielded seeds and nonsignificant increases in

flavonoids in the yielded canola seeds either in plants irrigated with 75% FC or 50% FC relative to corresponding controls. The increases in seed yield/plant due to 20 mM GB were 30.80% and 60.28% at 75% FC and 50% FC, respectively, relative to corresponding controls. The fatty acid profile of canola oils showed different responses to GB treatments either in unstressed plants or drought-stressed plants. Oleic and linoleic acids were increased accompanied by decreases in linolenic and erucic acids under the interaction effect of GB treatments and drought stress (75% FC and 50% FC), and these results led to decreases in total saturated fatty acid and increases in unsaturated fatty acid relative to corresponding controls. Generally, 20 mM GB was the most pronounced and effective treatment in alleviating the deleterious effect of moderate or severe drought stress on canola plants. Meanwhile, 60 mM GB had the most pronounced effect on tolerance to salinity stress in safflower seedling. The GB-increased tolerance to salt in safflower was mainly related to increased CAT and SOD activities and the prevention of cell membrane damage as a result of reduced lipid peroxidation and improved ion homeostasis under salinity stress condition (Alasvandyari et al. 2017).

10.9.2 Proline

It is evident from different reports that application of proline induces abiotic stress tolerance in plants (Ali et al. 2007; Taie et al. 2013; Dawood et al. 2014). Its further role in salinity appears to involve the induction of salt-responsive genes, with the resultant formation of new proteins which may improve the adaptation to salinity stress (Khedr et al. 2003). Moreover, proline may be having a role in stabilization of cellular proteins and membranes in presence of high concentrations of osmotic stress. Proline accumulation in plants could be only useful as a possible drought injury sensor instead of its role in stress tolerance mechanism (Jahari et al. 2010). In addition, Vendruscolo et al. (2007) reported that proline is involved in tolerance mechanisms against oxidative stress, and this is the main strategy of plants to avoid detrimental effects of water stress. Proline plays an important role as a sink for energy to regulate redox potentials (Simiroff and Cumbes 1989), alleviates salt stress induced by enhancement in oxygenase and carboxylase activities of Rubisco (Sivakumar et al. 2000), and protects plants from free radical that induced damage by quenching of singlet oxygen (Matysik et al. 2002). Several functions are proposed for the accumulation of proline in tissues exposed to salinity stress: osmotic adjustment (Voetberg and Sharp 1991), C and N reserves for growth after stress relief (Hellmann et al. 2000), detoxification of excess ammonia (Skopelitis et al. 2006), stabilization of proteins and membranes (Mansour 1998), protection of macromolecules from denaturation (Hamilton and Heckathorn 2001), osmoprotection (Kishor et al. 1995), free radical scavenging (Chen and Dickman 2005), antioxidation (Hoque et al. 2007), and regulation of cytosolic acidity (Sivakumar et al. 2000).

Taie et al. (2013) mentioned that pre-sowing seed treatment with proline seems to enhance faba bean salt tolerance via improving growth parameters, photosynthetic pigments, soluble carbohydrate, and total carbohydrate; meanwhile phenolic,

proline, Na⁺, and Cl⁻ contents were decreased relative to their corresponding salinity controls. Proline treatments induced over expression for new protein bands with high density.

10.10 Seed Priming with Melatonin

Melatonin (N-acetyl-5-methoxytryptamine) is an indolic compound (biogenic indoleamine) structurally related with other important substances, such as tryptophan, serotonin, indole-3-acetic acid (IAA), etc. Several authors hypothesized that melatonin may possess some auxin-like effects and may act as a regulatory molecule in plants (Van Tassel et al. 2001). Many evidences have shown melatonin could alleviate biotic and abiotic stresses such as temperature, salinity, light, drought, and pathogen (Li et al. 2012; Zhang et al. 2013a, b, 2014; Meng et al. 2014). Moreover, melatonin also could regulate the expression of a large number of genes involved in plant stress defense (Weeda et al. 2014; Zhang et al. 2014). Melatonin application could be a good bio-stimulator improving not only seed germination and seedling/plant growth but also crop production especially under stress conditions (Janas and Posmyk 2013). Melatonin is soluble in both water and lipid so it may act as a universal hydrophilic and hydrophobic antioxidant (Janas and Posmyk 2013). Tan et al. (2007) mentioned that elevated levels of melatonin probably protect plants against water and soil pollutants through acting as a direct free radical scavenger and as an indirect antioxidant. One melatonin molecule may scavenge up to ten free radicals (Tan et al. 2007), which contrasts with the classic antioxidants that typically detoxify one radical per molecule. Its antioxidant activity may manifest itself in several ways: (1) direct free radical scavenging, (2) elevating the antioxidant enzyme activity, (3) protecting antioxidant enzymes from oxidative damage, (4) increasing the efficiency of mitochondrial transport chain, and (5) reducing the generation of free radicals (Tan et al. 2010). Paredes et al. (2009) reported that melatonin functions in plants can be recognized into three categories: growth promoters as auxins, antioxidants for free radicals which serve as a first-line defense against oxidative stress, and other functions (signal molecules for circadian maintenance, regulation of flower development, or maintenance of developmental stages in fruit tissues). Hernandez-Ruiz et al. (2004) mentioned that a higher concentration of melatonin (200 μM) had no significant effect or even inhibitory effect on seed germination. However, lower concentrations of melatonin (50 or 100 μM) promoted seed germination as mentioned by Wei et al. (2015).

Pretreatment of melatonin attenuates cold-induced apoptosis in carrot suspension cells (Lei et al. 2004) and decreased lipid peroxidation caused by toxic copper ion in red cabbage seedlings (Posmyk et al. 2008). Melatonin prevented chlorophyll degradation during the senescence of barley leaves (Arnao and Hernandez-Ruiz 2009) and protected membrane structures against peroxidation during chilling stress and recovery in cucumber seeds (Posmyk et al. 2009). Posmyk et al. (2008) reported that the pre-sowing seed treatment with melatonin-protected red cabbage seedlings against toxic Cu ion concentrations as well as melatonin application to cucumber

seeds had a beneficial effect on seed germination, the growth of seedlings, and crop production of plants especially those subjected to cold stress (Posmyk et al. 2009) and water stress (Zhang et al. 2013a, b). Jiang et al. (2016) mentioned that seed priming with 0.8 mM melatonin alleviates the salinity damage to maize by improving SOD, CAT, and PAL activities, relative water content, and proline and total phenolic contents and decreasing membrane relative electrolyte leakage and lipid peroxidation product. Szafrańska et al. (2012) and Jiang et al. (2016) mentioned that either seed priming or exogenous application with melatonin significantly increased PAL activities and total phenolic content. Janas and Posmyk (2013) showed that hydroprimed or osmoprimed seeds of corn (*Zea mays* L.), mung bean (*Vigna radiata* L.), and cucumber (*Cucumis sativus* L.) with melatonin had higher crop yield than the control ones under field conditions, since the production of corn, cucumber, and mung bean primed with melatonin was about 10–25% greater in comparison to those primed without melatonin and is dependent on plant species. Zhang et al. (2013b) reported that 100 μM melatonin alleviated polyethylene glycol-induced inhibition of cucumber seed germination, showing the greatest germination rate and photosynthetic rate, and at the same time significantly reduced chlorophyll degradation. Furthermore, the ultrastructure of chloroplasts in water-stressed cucumber leaves was improved after melatonin treatment, thus reversing the effect of water stress. Szafrańska et al. (2014) mentioned that hydropriming *Vigna radiata* seeds with melatonin (50 μM L^{-1}) increased level of melatonin in roots derived from hydroprimed seeds with melatonin by sevenfold higher than roots derived from non-primed seeds. Wei et al. (2015) concluded that coating soybean seeds with melatonin promoted soybean plant growth, increased yield, and improved salinity stress tolerance. Recently, Dawood and EL-Awadi (2015) concluded that melatonin treatments (100 and 500 mM) improved growth parameters, relative water content, photosynthetic pigments, and total carbohydrate, total phenolic, indoleacetic acid, K$^+$, and Ca^{+2} contents and reduced the levels of compatible solutes and Na$^+$ and Cl$^-$ contents in leaf tissues of faba bean plants irrigated with diluted seawater (3.85 and 7.69 dS/m). Melatonin at 500 mM had a more pronounced effect in alleviating the adverse effects of the two salinity levels on the performance of faba bean plants than 100 mM melatonin. The beneficial effects of melatonin treatments in alleviating the harmful effect of salinity stress on the growth parameters were more pronounced in the plants grown under the higher salinity level (S2 = 7.69 dS/m) than those grown under lower salinity level (S1 = 3.85 dS/m) relative to corresponding controls. The increases in total photosynthetic pigments were 22.31%, 12.87%, and 15.85% in the plants treated with 500 mM melatonin and irrigated with tap water (S0) and diluted seawater at lower (S1) and higher (S2) concentrations, respectively, as compared with corresponding controls.

Jiang et al. (2016) suggest that seed priming with 0.8 mM melatonin significantly improved germination energy, germination percentage, seedling vigor index, shoot and root lengths, seedling fresh and dry weights, K+ content, relative water content, proline and total phenolic contents, superoxide dismutase, and catalase and phenylalanine ammonia lyase activities and significantly decreased mean emergence time, Na+ content, electrolyte leakage, and malondialdehyde content compared with

untreated seeds under salinity stress; thereby seed priming with melatonin alleviates the salinity damage to maize.

10.11   Seed Priming with Plant Extract

The allelopathic action of various natural compounds on the growth and development of many plants may be inhibitory or stimulatory depending on their concentration in the surrounding medium and on their physiological activity within plants (El-Daly and Soliman 1997). Allelochemicals like phenolic compounds, flavonoids, terpenoids, alkaloids, steroids, and other compounds, sometimes have a greater allelopathic effect than individual compound alone. Einhellig (1995) mentioned that these metabolites may be selective in their action or plants may be selective in their responses. Moreover, allelochemicals which inhibit the growth of some species at certain concentrations may stimulate the growth of the same or different species at different concentrations (Narwal 1994). These allelochemicals promote or inhibit the crop growth based on species-specific concentrations (Ambika et al. 2003). Phenolic compounds can act on enzymes, phytohormone activity, and mineral content (Einhellig 2004). Saponins are readily soluble in water which may enhance the nutrient absorption (Satish et al. 2007). Alkaloids, phenolic compounds, and saponins protect the plants against pathogens and also produce antioxidant activity.

Leaves of different plants contain alkaloids and phenolic compounds which protect the plants against pathogens and also produce antioxidant activity (Satish et al. 2007). Rathinavel and Dharmalingam (1999) mentioned that the presence of bioactive substances in the leaf extracts enhanced lipid utilization and enzyme activity that increased dry weight and development of seedling to reach autotropic stage, enabling them to produce relatively more quantity of dry matter which is discerning the cause for the hike in vigor index by hardening treatment. It is generally assumed that physiologically active substances might have activated the embryo and other associated structures which resulted in the absorption of more water due to cell wall elasticity and development of stronger and efficient root system, and that would have ultimately resulted in higher vigor index (Rangaswamy et al. 1993). Many researchers also reported the benefits of seed hardening with different medicinal plants leaf extract to overcome the adverse condition (Renugadevi et al. 2008; Kamaraj and Padmavathi 2012).

It is worthy to mention the most important plants containing allelochemicals as follows: *Chlorophytum* leaves are high in saponin, carbohydrate, proteins, and various alkaloids (Chakraborthy et al. 2014). Leaves of *Vinca rosea* are also high in alkaloids and phenolic compounds (Tiong et al. 2013). Neem leaves contain flavonoids, steroids, carbohydrates, glycosides, antiquinone, terpenoides, and alkaloids (Raphael 2012). The seeds of fenugreek contain lysine and L-tryptophan-rich proteins, mucilaginous fiber, and other rare chemical constituents such as saponins, coumarin, fenugreekine, nicotinic acid, sapogenins, phytic acid, scopoletin, and trigonelline (Bukhari et al. 2008). Furthermore, intercropping fenugreek with faba bean can reduce *Orobanche crenata* infection (Fernández-Aparicio et al. 2006).

Guava leaf contains volatile oil such as quercetin, avicularin, guaijaverin, etc. (Morant et al. 2008). Previous studies on the chemical composition of guava leaves have identified chemical products belonging to the groups with allelopathic properties (Monteiro and Vieira 2002) such as terpenoids, flavonoids, coumarins, and cyanogenic acids, among others (Gutiérrez et al. 2008). *Some studies have already identified guava allelopathic effects on other species, the effect of guava fruit extracts on cucumber germination* (*Cucumis sativus*) (Bovey and Diaz-Colon 1968) as well as the effect of guava root exudates on lettuce (*L. sativa*) germination and root growth and the root growth of bristly foxtail (*Setaria verticillata*) (Brown et al. 1983). Chapla and Campos (2010) reported that allelopathic effect of the guava leaf aqueous extract on the germination and growth of lettuce occurred only at 20% concentration. Regarding *Lantana camara*, *their* leaves, roots, and fruits contain allelochemicals mainly phenolics, flavonoids, tannins, and carbohydrates as mentioned by Gopie-shkhanna and Kannabiran (2007). Moreover, Basu and Hazra (2006) indicated that lantana plant has strong antioxidant activities. Yi et al. (2005) reported the presence of several phenolic compounds in lantana leaf extract identified by HPLC as salicylic, gentisic, β-resorcylic, vanillic, caffeic, ferulic, and p-hydroxybenzoic acids, coumarin, and 6-methylcoumarin. Ahmed et al. (2007) found that different concentrations of aqueous leaf extracts of lantana caused significant inhibitory effect on germination, root and shoot elongation, and development of lateral roots of receptor crops. The inhibitory effect was much pronounced in root and lateral root development rather than shoot and germination. Earlier, Dawood and Taie (2009) soaked lupine seeds with freshly prepared aqueous leaf extract (5, 10, 15% w/v) of eucalyptus and lantana separately for 24 h. The phenolic compounds and flavonoids (allelochemicals) are detected in higher amounts in aqueous leaf extract of eucalyptus than that of lantana. Aqueous leaf extract of either lantana or eucalyptus caused a gradual decrease in germination % of both sweet and bitter lupine varieties. Their effect was proportional to the extract concentration. Germination % increased by extending the germination period. Phenolic and alkaloid contents of 9-day-old seedlings increased by all treatments. All applied treatments had positive effect on photosynthetic pigments and yield as well as protein, carbohydrate, ash, and phenolic contents of the yielded seeds, whereas alkaloid % decreased. In respect to oil content, it was decreased by lantana treatments. Moreover, Dawood et al. (2012) mentioned that incorporated 10% fenugreek seeds or 20% guava leaves or 20% lantana leaves into the soil caused significant increases in the photosynthetic pigments (chlorophyll a, chlorophyll b and carotenoid) and the total carbohydrate content of sunflower leaf tissues accompanied by a significant decrease in the total phenolic content. The head weight, seed weight/head, and 100-seed weight were increased in the following order: fenugreek treatment > lantana treatment > guava treatment. It was noted that fenugreek treatment is the most effective treatment in increasing oil % followed by guava treatment, while the lowest increase resulted from lantana treatment. Fenugreek treatment caused the highest decrease in (C16:0 + C18:0) accompanied by the highest increase in (C18:1 + C18:2). Regarding the total essential amino acids, it was noticed that fenugreek treatment showed a noticeable increase, whereas lantana and guava treatments

showed a decrease in total essential amino acids. Phuwiwat et al. (2012) concluded that leaves of *Melia azedarach* contained water soluble allelochemicals that caused inhibition of both water uptake and α-amylase activity of *E. crus-galli* during germination process. Prabha et al. (2016) concluded that seed priming with 2% leaf extract of *Chlorophytum*, *Agel*, *Azadirachta*, and *Vinca* were found suitable to enhance seedling vigor and reduce mortality rate in the presence of *Fusarium oxysporum* in tomato. Seed priming with these plant leaf extracts is cost-effective and easy to apply at farmer's field and is suitable under "organic farming" framework.

10.12 Seed Priming with Chitosan

Chitosan is an abundant and relatively cheaper cationic polysaccharide obtained as waste material during seafood processing (Guan et al. 2009). Chitosan application to peanut seeds increased levels of germination percentage, energy, lipase activity, gibberellic acid (GA3), and indoleacetic acid (IAA) (Zhou et al. 2002). Chitosan has been proven to act as a positive factor in enhancing shoot and root length, fresh and dry weights of shoots, and roots and leaf area in bean plants watered with the chitosan solution (Sheikh and AL-Malki 2011). Moreover, it is evident that chitosan has some potential under stressful environment. Chitosan-coated seeds have been reported to demonstrate accelerated germination and tolerance to stress in hybrid rice (Ruan and Xue 2002) and enhanced vigor of maize seedlings (Shao et al. 2005). Furthermore, chitosan priming improved maize germination and seedling growth in relation to physiological changes under low-temperature stress (Guan et al. 2009) and improved the germination of plants under drought stress (Suchada et al. 2007). Moreover, chitosan priming under stress resulted in highly improved germination index and reduced germination time to promote early seedling establishment and synchronized growth in rice (Suchada et al. 2007) and maize (Guan et al. 2009). Sadeghi et al. (2011) mentioned that the improvement in germination and vigor of soybean plant was probably due to the reserve mobilization of food material, activation and resynthesis of some enzymes, and DNA and RNA synthesis which started during osmotic priming. There is possibility that similar germination-responsive genes may be activated because of chitosan priming under osmotic stress. Hameed et al. (2014) observed that chitosan priming treatments not only improved seed germination but also enhanced wheat seedling growth under osmotic stress induced by PEG. Its beneficial effects on germination and seedling vigor provided evidence that chitosan is a promising seed priming agent for the improvement of osmotic stress tolerance in wheat.

10.13 Seed Priming with Polyethylene Glycol (PEG)

Polyethylene glycol (PEG) as an inert material can prevent embryo toxicity problems during priming (Cantliffe 1983). The large size of PEG molecule (6000–8000 mw) also prevents its penetration into seed tissues, avoiding lowering the

osmotic potential (Brocklehurst and Dearman 1984). Osmopriming with polyethylene glycol is most commonly used to induce either osmotic stress varying between −0.5 MPa (sweet corn, Ghiyasi et al. 2008) and −2 MPa (sunflower, Bailly et al. 2000; sugar beet, Capron et al. 2000) in plants or water-deficit condition because it is not naturally produced in the plant tissue and cannot penetrate into cell from the media. Soaking seeds before sowing with PEG solution helps to initiate the membrane repairing systems and metabolic preparation for germination via controlling the water absorption rate of seeds (Jisha et al. 2013). Massarat et al. (2014) concluded that priming with PEG 6000 had beneficial effects on germination and seedling establishment of corn seeds under drought and saline conditions, whereas the major disadvantage resulting from the use of PEG is the reduction of oxygen in the solution, because of its viscosity (Mexal et al. 1975), so aerating the solution during PEG osmopriming can overcome this problem (Bujalski and Nienow 1991).

10.14 Seed Priming with Inorganic Salts

10.14.1 NaCl

It has been shown that NaCl seed priming could be used as an adaptation method to improve salt tolerance of seeds. Sivritepe et al. (2003) and Yildirim et al. (2011) concluded that NaCl seed priming improves seed germination, seedling emergence, and growth under saline conditions. The benefits of NaCl seed priming did not persist beyond the seedling stage in cucumber (Passam and Kakouriotis 1994), while Cano et al. (1991) concluded that NaCl seed priming had positive effects on mature plants and on yield of tomato. According to Cano et al. (1991), the higher salt tolerance of plants from primed seeds seems to be the result of a higher capacity for osmotic adjustment since plants from primed seeds have more Na^+ and Cl^- ions in their roots and more sugars and organic acids in leaves than plants from non-primed seeds. Moreover, priming canola seeds with NaCl solution increased seedling cell membrane stability and decreased seedling damage under salinity condition due to increased seedling K^+ and proline content (Farhoudi et al. 2007). Massarat et al. (2014) observed that priming corn seeds with NaCl had beneficial effects on germination and seedling establishment under drought and saline conditions. Omami (2005) suggested that priming of amaranth seeds with NaCl improve cell membrane stability and decrease MDA production and increased salt tolerance by promoting K^+ and Ca^{2+} accumulation.

10.14.2 KNO3

The beneficial effects of seed priming with KNO_3 solution on seed germination under salinity conditions have been observed in sunflower (Kaya and Day 2008;

Farhoudi 2014) and muskmelon (Nascimento 2003). Singh and Rao (1993) reported that KNO_3 priming effectively improved germination, seedling growth, and seedling vigor index of the seeds of sunflower varieties with low germination. Improving seedling sunflower growth by KNO_3 priming under salinity condition can suggest nontoxify of KNO_3 due to ion accumulation in the embryo (Kaya et al. 2006). Mauromicale and Cavallaro (1996) mentioned that seed priming of herbage grasses with KNO_3 solution decreased the mean germination time as compared to PEG solution because of KNO_3 did not have toxicity and did not prevent water uptake. Farhoudi (2014) showed that priming of sunflower seeds with 0.6 and 0.9 MPa KNO_3 solution was more effective than non-priming seeds under salinity condition and demonstrated its potential effect in improving tolerance to salinity by increasing seedling fresh weight and POX enzyme activity accompanied by decrease in seedling MDA concentration compared to non-priming seeds.

10.14.3 Sodium Silicate

Evidences have proved that sodium silicate treatment improved the cell membrane stability by reducing the lipid peroxidation in different plants under abiotic stresses (Liang et al. 2007; Pei et al. 2010; Wang et al. 2011). Sodium silicate resulted in improved germination, growth, and antioxidant enzyme activities and reduced lipid peroxidation during drought stress in wheat (Pei et al. 2010; Ali et al. 2012). Moreover, sodium silicate treatment lowered down the oxidative stress by enhancement of antioxidant production (glutathione reductase, catalase, peroxidase, and superoxide dismutase) during drought stress in wheat, barley, and soybean plants (Liang et al. 2003; Gong et al. 2005; Miao et al. 2010; Wang et al. 2011). Moreover, sodium silicate application has been reported to enhance the germination and nutrient use leading to better seedling development in soybean (Miao et al. 2010). Hameed et al. (2013) mentioned that seed priming with sodium silicate not only improved the seed germination and seedling vigor but also enhanced the wheat seedling growth under water-deficit stress induced by PEG.

It is worthy to mention that the accumulation of salts in the seed could be toxic (Bradford 1995), reduce the osmotic potential, and induce a high water absorption during treatment (Parera and Cantliffe 1994), resulting in a more likely radicle protrusion. In addition, effects of inorganic salts on germination are different from those carried out by PEG, depending on seed species. For instance, osmopriming with inorganic salts was toxic to sorghum seeds (Haigh and Barlow 1987), whereas it was effective as PEG in asparagus (Pill 1995) and performed better as PEG in tomato (Mauromicale and Cavallaro 1997). The difference in the response of different species to salts or PEG may be due to a selective semipermeable layer that surrounds the embryo: when this layer is present, it allows the absorption of water, but prevents salt diffusion; when it is absent, ions can be absorbed and cause embryo damages (Welbaum et al. 1998). For example, tomato (*Solanum lycopersicum* L.), melon (*Cucumis melo* L.), lettuce (*Lactuca sativa* L.), and *Capsicum annuum* seeds possess this layer and may be safely subjected to osmopriming with inorganic salts

(Welbaum and Bradford 1990). Conversely, this treatment is harmful to broccoli and cabbage seeds (*Brassica oleracea* L.), which lack this layer (Taylor et al. 1997).

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