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Seed Priming with Plant Growth Regulators to Improve Crop Abiotic Stress Tolerance

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Abstract

Plants are frequently subjected to abiotic stress such as drought, salinity, heat, and cold which constitutes a major limitation to agricultural production worldwide. The unfavorable environmental conditions that plants encounter in vegetative cycle perturb their metabolic reactions and negatively affect growth at cellular and biochemical plant levels. Preventing crop losses and generating more food to meet the demands of growing human populations have gained importance. Identifying plant mechanisms to neutralize abiotic stresses and sustain their growth and survival under unfavorable conditions holds huge importance. Research studies have revealed that plant growth regulators (PGR) confirm their significance as metabolic engineering targets for producing abiotic stress-tolerant crop plants. In addition, seed priming has shown its importance as a powerful technique to improve germination, growth, and yield of crops under unfavorable environment conditions. The combination of the two effects, seed priming with PGR, could have very prevailing results. In this context, during this chapter, we evaluate the effect of seed priming with PGR in plant growth development and abiotic stress tolerance.

Keywords

Abiotic stress · Seed priming · Plant growth regulators · Growth · Germination

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6.1 Introduction

The human population is growing rapidly and requires a considerable increase in agricultural productivity worldwide. However, diverse abiotic stresses are limiting crop productivity (Wani and Sah 2014). In order to nourish the rising world population, crop productivity must be amplified in the near future. That's why plant breeders and biotechnologists should improve crop tolerance to abiotic stress by recognizing these mechanisms. However, plant machineries leading to environmental stress response and tolerance are complex (Qin et al. 2011). Since the complication of stress tolerance, conventional breeding trials have met little success. That's why original and effective approaches should be developed. Seed priming is a revolutionary technique used to improve seed germination and seedling growth in abiotic stress conditions. During this process, a series of physiological and biochemical processes are triggered leading to improving plant growth under stress conditions (Eisvand et al. 2010). Seeds can be soaked in solutions containing exogenous molecules such as salts (Khan et al. 2009a, b) or plant growth regulators (PGR) (Nakaune et al. 2012). Seed priming with PGR pretreatment is a commonly used strategy to improve seed germination and seedling growth in unfavorable conditions (Masood et al. 2012; Hu et al. 2013). Seeds presoaked with optimal concentration of PGR enhance germination, growth, and yield of crops under stress condition by rising nutrient reserves through improved physiological activities and root profusion (Afzal et al. 2002; Akbari et al. 2007). PGR are organic compounds produced in extremely small amount and play a vital function in growth, expansion, and yield of crops. They regulate, as chemical messengers, a range of cellular processes in higher plants and coordinate diverse signal transduction pathways during abiotic stress response (Vob et al. 2014; Kazan 2015). For instance, seeds of rye (*Secale montanum*) pretreated with gibberellic acid (GA3) increased germination under water deficit (Ansari et al. 2013). Khan et al. (2009a, b) confirmed that pepper seeds (*Capscum annum* L.) pretreated with salicylic acid resulted in better germination and seedling growth under salt stress. Furthermore, ethylene reduces high temperature effect on seed germination of lettuce (Nascimento et al. 2004).

6.2 Abiotic Stresses: World Agricultural Challenge

Exploring how abiotic stresses can influence plant growth at the physiological, biochemical, and molecular levels is decisive to advance crop production, since stresses cause crop losses (Kazan 2015). Abiotic stresses, including drought, salinity, chilling, freezing, heat, and UV radiation, are the main environmental factors restraining crop production. They negatively influence growth, biomass production, and yields of food crops threatening consequently food security worldwide (Kaur et al. 2008; Thakur et al. 2010). Among these stresses, drought, salinity, and temperature severity are the most common abiotic stresses limiting crop productivity in the world (Jaleel et al. 2009; Thakur et al. 2010). They affect plant survival, pigment content, membrane integrity, water relations, osmotic adjustments, and photosynthetic activity (Sanghera et al. 2011; Pathak et al. 2014). Drought and salinity affect together more than 55% of the world's agricultural land (Dos Reis et al. 2012). Since abiotic stress tolerance is multigenic in nature (Collins et al. 2008), an enormous challenge was undertaken to comprehend key mechanisms to go forward in selective breeding purposes. Understanding the machinery of plants' environmental stress tolerance is of critical importance for the development of stress-tolerant and high-yielding food crop cultivars.

6.2.1 Plant Drought Tolerance

Drought tolerance is the ability to survive and produce stable yields under water scarcity. Drought stress decreases plants' photosynthetic rate, decreasing consequently the amount of assimilates available for export to the sink organs (Kim et al. 2000). Abscisic acid (ABA) is a key plant growth regulator in the response and adaptation of plants to water scarcity. It is involved in stomatal closure, accumulation of osmoprotectants, and changes in gene expression (Umezawa et al. 2010). The biosynthesis of osmoprotectants such as amino acid, amines, and carbohydrates is another indispensable strategy for plant resistance to water stress. The most common osmoprotectants are proline, glycine betaine, fructans, starch, and mono- and disaccharides.

6.2.2 Plant Heat Tolerance

Heat stress perturbs cellular homeostasis and causes protein denaturation and dysfunction in plant cells, leading to brutal growth retardation. During this stress, electron transport is altered affecting electron flow from oxygen-evolving complex (OEC) toward the acceptor side of photosystem II (PSII). These alterations affect the generation of ATP, Rubisco for carbon fixation, and starch (Asthir 2015). Drought stress generates the accumulation of ROS leading to a severe damage in DNA and peroxidation of membrane lipids and pigments. Other changes include a decrease in photosynthetic pigment ratio and inhibitions of stomatal conductance and photosynthesis rate. These alterations ultimately reduce the partitioning of photosynthates, which manifest by reduced growth and economic yield. Other morphological damages associated with heat stress comprise scorching of leaves, branches, and stems, leaf senescence, fruit discoloration, and damage (Hasanuzzaman et al. 2013).

6.2.3 Plant Cold Tolerance

Cold stress occurs at temperatures less than 20 °C. Chilling (<20 °C) or freezing (<0 °C) temperatures can trigger the formation of ice in plant tissues, cause cellular dehydration and leakage of intracellular solutes, and reduce plasma membrane integrity (Chinnusamy et al. 2007). Consequently, cold stress severely affects plant growth and leads to substantial crop losses (Sanghera et al. 2011). To cope with this unfavorable condition, plants adopt several strategies such as activating primary metabolisms, raising the level of antioxidants, and maintaining osmotic balance (Miura and Furumoto 2013). During cold stress, membrane rigidification occurs as opposed to heat stress. This process is the upstream trigger for the induction of cytosolic Ca^{2+} signatures leading to a transient increase in cytosolic Ca^{2+} levels (Knight et al. 1991).

6.3 Plant Growth Regulators: Key Mediators of Plant Responses to Environmental Stresses

Plants have to adjust their development to respond to various abiotic stresses. Plant growth regulators (PGR) are cells signaling molecules acting in very small quantities that mediate these responses. Their crucial functions are advancing plant adaptation to an altering environment by mediating growth, development, and nutrient allocation (Fahad et al. 2015a, b). PGR are endogenous substances responsible in adjusting physiological and molecular responses for plant survival. They include gibberellins (GAs), salicylic acid (SA), auxin (IAA), ethylene (ET), cytokinins (CKs), brassinosteroids (BRs), abscisic acid (ABA), and jasmonates (JAs).

6.3.1 Abscisic Acid (ABA), the Abiotic Stress Hormone

Abscisic acid (ABA) is the most studied PGR. It plays an important role throughout numerous plant physiological processes and developmental stages including stomatal closure, embryo morphogenesis, seed dormancy, and synthesis of storage proteins and lipids (Sreenivasulu et al. 2010). ABA is a vital messenger in the adaptive response of plants to abiotic stress. During this response, endogenous ABA levels increase rapidly, activating specific signaling pathways and altering gene expression levels (O'Brien and Benkova 2013). Zhang et al. (2006) and Hossain et al. (2010) stated a substantial increase in ABA concentration upon exposure of plants to salinity and drought. It regulates the expression of different stress-responsive genes implicated in the accumulation of compatible osmolytes and the synthesis of proteins and antioxidant enzymes (Chaves et al. 2003; Verslues et al. 2006).

6.3.2 Auxins (IAA)

IAA (indole-3-acetic acid) is a multifunctional PGR and is vital for plant growth under stress conditions (Kazan 2013). IAA boosts plant root and shoot growth and plays consequently a fundamental part in plant adaptation to salt stress (Egamberdieva 2009; Iqbal et al. 2014; Fahad et al. 2015a, b). Auxin stimulates the transcription of primary auxin response genes identified and characterized in several plant species (Javid et al. 2011).

6.3.3 Gibberellins (GAs)

GAs improve seed germination, leaf expansion, stem elongation, fruit development, and abiotic stress response and adaptation (Yamaguchi 2008; Colebrook et al. 2014). It interacts with other PGR in many stimulus-response processes (Munteanu et al. 2014).

6.3.4 Salicylic Acid (SA)

SA plays a vital role in the regulation of plant growth, ripening, and responses to abiotic stresses (Khodary 2004; Miura et al. 2013; Miura and Tada 2014). Gharib and Hegazi (2010) showed that SA stimulated growth of bean seedlings and reduced the adverse effect of cold and chilling stresses.

6.3.5 Cytokinins (CKs)

CKs are involved in many plant growth processes and abiotic stress tolerance (Nishiyama et al. 2011; Kang et al. 2012; O'Brien and Benkova 2013). CKs are often considered ABA antagonists (Pospíšilová 2003). It has been linked to different abiotic stress tolerance like cold stress and freezing stress (Jeon et al. 2010). Salinity or osmotic stress shows an effect in the expression levels of CK receptors and metabolism, respectively, in *Arabidopsis* and maize (Zalabák et al. 2013).

6.3.6 Jasmonates (JAs)

Jasmonates are involved in plant development including reproductive processes, secondary metabolism, and plant responses to environmental stresses (Pauwels et al. 2009; Seo et al. 2001; Fahad et al. 2015a, b). Exogenous application of JA significantly reduced salinity and heavy metal stress symptoms in plants by activating the antioxidant machinery (Yoon et al. 2009; Yan et al. 2013). Wang et al. (2010) have reported a significant increase in endogenous levels of JA in rice roots under salinity stress. In addition, JA confers tolerance to metal stress in plants via the accumulation of phytochelatins (Maksymiec et al. 2007).

6.3.7 Ethylene (ET)

ET, a gaseous PGR, is involved in plant growth and development, notably fruit ripening, flower senescence, leaf and petal abscission, and stress response regulation (Gamalero and Glick 2012; Groen and Whiteman 2014). Enhanced abiotic tolerance was achieved with higher endogenous ET concentrations in plants (Shi et al. 2012; Groen and Whiteman 2014). ET also induces plants' defense response to heat stress (Larkindale et al. 2005). Yin et al. (2015) have shown that ET and ABA act in synergy or in antagonism to control plant growth.

6.4 Seed Priming as a Strategy to Improve Abiotic Stress Tolerance

Recently, diverse strategies have been employed to induce abiotic stress tolerance in plants. Seed priming is an effective, practical, and low-cost technique to obtain rapid emergence, high seedling vigor, and better crop yields under unfavorable environmental conditions (Jisha et al. 2013; Paparella et al. 2015). It is a controlled hydration technique triggering metabolic processes during early phase of germination before radicle protrusion (Hussain et al. 2015). Higher and synchronized germination of primed seeds is due to reduction in the lag time of imbibition (Brocklehurst and Dearman 2008), enzyme activation (Lee and Kim 2000), buildup of germination-enhancing metabolites (Hussain et al. 2015), metabolic repair during imbibition (Farooq et al. 2006), and osmotic adjustment (Bradford 1986). Primed plants exhibit activation of cellular defense responses, which imparts abiotic stress tolerance (Jisha et al. 2013). Various seed priming techniques have been employed under different environmental stresses including hydropriming, osmopriming, chemical priming, nutrient priming, and hormonal priming (Jisha et al. 2013; Paparella et al. 2015). During seed priming, germination process is induced by soaking seeds in solutions containing exogenous molecules such as salts (Khan et al. 2009a, b), metals (Mirshekari et al. 2012), or hormones (Nakaune et al. 2012). Varier et al. (2010) and Eisvand et al. (2010) suggest that seed priming activates a series of physiological processes that improve plant growth under stressful conditions, including the induction of antioxidant systems.

6.4.1 Seed Priming with Plant Growth Regulators

PGR pretreatment is a commonly used priming approach to improve seed germination under stressful conditions (Jisha et al. 2013; Hu et al. 2013). It can be used to advance germination, seedling growth, and yield under drought, salinity, metal, cold, and heat stresses.

6.4.1.1 Seed Priming with PGR Under Water Deficit

Seeds of rye (*Secale montanum*) primed with gibberellic acid increased germination under water deficit (Ansari et al. 2013). ABA-primed seeds of *Brassica napus* exhibited earlier germination and higher final percent radicle protrusion than non-primed control seeds, under water stress (Gao et al. 2002). Seeds of *Agropyron elongatum* primed with gibberellin and abscisic acid exhibited induced CAT and SOD activities under drought conditions when compared to unprimed seeds (Eisvand et al. 2010). Farooq et al. (2013) have shown that seeds primed with ascorbic acid improve emergence, growth, yield, and water statue of wheat seedlings under water deficit. Priming with ascorbic acid showed significant effects on germination percentage, shoot length, root length, vigor index, and CAT and POX activity in rapeseed (*Brassica napus* L.) plant under drought condition (Razaji et al. 2014).

6.4.1.2 Seed Priming with PGR Under Salt Stress

In pepper (*Capscum annum* L.), Khan et al. (2009a, b) showed that pretreatment with acetylsalicylic acid and salicylic acid resulted in greater uniformity of germination and establishment of seedlings under high salinity. ABA-primed seeds of *Brassica napus* exhibited earlier germination and higher final percent radicle protrusion than non-primed control seeds, under salt stress (100 mM NaCl) (Gao et al. 2002). In wheat seed germination, auxin pretreatments increased the hypocotyl length, seedling fresh and dry weight, and hypocotyl dry weight under saline conditions (Akbari et al. 2007). Salicylic acid priming in fennel seeds also showed better germination under salt stress (Farahbakhsh 2012). Iqbal et al. (2011) have reported that seed priming with gibberellic acid induced an increase in grain yield of wheat plants, modulation of ion uptake and partitioning, and hormone homeostasis under saline conditions.

6.4.1.3 Seed Priming with PGR Under Heat Stress

Additionally, ethylene was used to minimize the effect of high temperatures on seed germination of lettuce (*Lactuca sativa* L.) (Nascimento et al. 2004). Rehman et al. (2012) have shown that seed priming with salicylic acid improved temperature stress resistance in spring maize through an earlier emergence, increased seedling dry weight and tissue water status, and improved membrane stability. Seed priming with salicylic acid or jasmonic acid improves growth, carbohydrate content, and chilling resistance in sunflower (*Helianthus annuus* L.) (Gornik and Lahuta 2017). Singh and Singh (2016) have shown that seed priming with three levels of salicylic acid (0.25 mM, 0.5 mM, and 0.75 mM) improves growth, flowering, yield, and fruit quality under high-temperature stress conditions.

6.4.1.4 Seed Priming with PGR Under Cold Stress

The incorporation of methyl jasmonate (3 μM) into the priming solution on low temperature improves germination and emergence performance of watermelon (*Citrullus lanatus*) cv. Crimson Sweet (Korkmaz et al. 2004). Gamel et al. (2017) have shown that seed priming with 100 ppm gibberellic acid improves germination, growth, yield, and fruit quality of three tomato cultivars under low temperature. Ansari and Zadeh (2012) have shown that seed priming with gibberellic acid (25 ppm) advances germination and seedling growth of mountain rye (*Secale montanum*) under cold stress.

6.4.1.5 Seed Priming with PGR Under Metal Stress

Seed priming with ethylene (100 μM) improves germination parameters of pigeon pea under cadmium stress (Sneideris et al. 2014). PGR priming using auxin, cytokinin, and gibberellic acid at concentration of 10–100 μM was the most appropriate priming treatment for soybean (*Glycine max*) seeds grown under lead (Pb) stress conditions (Abu-Muriefah 2017). Seed priming with jasmonate advances growth and activity of SOD and POD and increases significantly the accumulation of chlorophyll and carotenoid and neutralizes the toxic effect of Cu^{2+} on *Cajanus cajan* seedlings under copper stress (Poonam et al. 2013).

6.5 Conclusion and Future Perspectives

It can be concluded that seed priming with PGR has the potential for improving crop abiotic stress tolerance which provides new opportunities to maintain sustainable crop production to feed the growing population under changing environmental conditions. Even though, with rapid development of genomic technology, significant attempts have been done on the way to decoding the plant abiotic stress responses, many challenges still lie ahead to uncover the complexity of stress signal transduction pathways. More hard work will be required at the genetic level of PGR biosynthetic pathway. The success in elucidating roles of PGR in stress tolerance at molecular levels will help in showing positive effects of seed priming with PGR and their substitutes in improving stress tolerance in a wide range of crop species. However, more research will be needed in unraveling the mechanism of PGR, especially with stress-responsive genes.

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