Physiological, Biochemical, and Molecular Aspects of Seed Priming

Sadam Hussain, Saddam Hussain, Abdul Khaliq, Shafaqat Ali, and Imran Khan

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Abstract Seed priming is a low-cost and effective strategy to enhance seed germination, vigor index, and yield in many field crops mainly under adverse environmental conditions. Seed priming is known to trigger the normal metabolic developments during early stage of germination, before the radicle protrusion. Higher, faster, and synchronized germination of primed seeds largely occurs due to enzyme activation, reduced imbibition time, metabolic reparation during imbibition, buildup of germination-promoting metabolites, and osmotic adjustment. Moreover, plants emerging from primed seeds exhibit faster activation of cellular defense systems, which trigger tolerance against consequent exposure to environmental stresses in the field. Several seed priming approaches including hydropriming,

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S. Hussain · S. Hussain (✉) · A. Khaliq · I. Khan
Department of Agronomy, University of Agriculture Faisalabad, Faisalabad, Punjab, Pakistan

S. Ali
Department of Environmental Sciences and Engineering, Government College University Faisalabad, Faisalabad, Pakistan

M. Hasanuzzaman, V. Fotopoulos (eds.), *Priming and Pretreatment of Seeds and Seedlings*, https://doi.org/10.1007/978-981-13-8625-1_3

nutrient priming, hormonal priming, chemical priming, osmopriming, and redox priming can be effectively used under different environmental conditions. The present chapter provides an overview of the physiological, biochemical, and molecular changes modulated by seed priming, which enhance seed germination and plant growth. Moreover, it discusses the possible mechanisms associated with seed priming-induced abiotic stress tolerance in plants.

Keywords Abiotic stresses · Antioxidants · Seed priming · Osmotic adjustment · Physiological and molecular mechanisms

Abbreviations

AQP	Aquaporin
AsA	Ascorbic acid
ATP	Adenosine triphosphate
BER	Base excision repair
CAT	Catalase
DEPs	Differentially expressed proteins
DHN	Dehydrins
GA	Gibberellin
GR	Glutathione reductase
H_2O_2	Hydrogen peroxide
HR	Homologous recombination
LEA	Late embryogenesis abundant
MT	Metallothionein
NaCl	Sodium chloride
NER	Nucleotide excision repair
OA	Osmotic adjustment
OP	Osmotic potential
PAs	Polyamines
PEG	Polyethylene glycol
POD	Peroxidases
Pro	Proline
ROS	Reactive oxygen species
RWC	Relative water contents
SOD	Superoxide dismutase

1 Introduction

Changes in climatic patterns have triggered the occurrence of biotic and abiotic stresses. These stresses are generally interrelated and cause undesirable morphological, biochemical, physiological, and molecular changes that affect the plant growth and development and ultimately the seed yield (Hussain et al. 2018a). Seed priming is an effective strategy to impart the abiotic stress tolerance besides strengthening the defense line of crop plants. In seed priming, presowing treatments are applied that control the hydration level within seed and allow pregerminative metabolic processes (physiochemical) to proceed while preventing radical emergence (Hussain et al. 2015; Lutts et al. 2016; Zheng et al. 2016; Hussain et al. 2018a). This phenomenon is described by an enhanced activation of plant defense mechanisms (Anderson et al. 2017). Stimuli from abiotic cues can prompt the priming establishment by acting as warning signals (Mauch-Mani et al. 2017). Upon stimulus perception, changes generally occur in the plant at the physiological, biochemical as well as at molecular levels.

Seed priming promotes the germination-related functions and enhances germination rate, vigor index, root length, photosynthetic efficacy, biomass production, and many other growth attributes in plants (Hussain et al. 2016a). Moreover, seed priming improves the plant biochemical status by induction and de novo synthesis of hydrolyses activity (e.g., α-amylase) and soluble sugar levels during germination process while nitrate reductase (NR) activity and N content in the growing seedlings under normal condition with respect to untreated seeds (Sharma and Bose 2006; Anaytullah and Bose 2007). Further, the definite role of priming in enhancing germination and growth of different crop plants under different abiotic stresses has been well established (Kaya et al. 2006; Zhang et al. 2006; Zhuo et al. 2009; Jisha et al. 2013; Paparella et al. 2015; Wang et al. 2016; Zheng et al. 2016; Hussain et al. 2018a, b). Seedlings emerged from primed seeds showed better antioxidative defense system owing to enhanced activities/levels of glutathione reductase (GR), catalase (CAT), peroxidases (POD), superoxide dismutase (SOD), and ascorbic acid (AsA), and regulation of stress protein like aquaporins (AQP), dehydrins (DHN), and late embryogenesis abundant (LEA) proteins (Wechsberg et al. 1994; Fashui 2002; Bolkhina et al. 2003; Anaytullah et al. 2012; Chen et al. 2013). In seed priming, seeds are hydrated in different types of solutions for the initiation of certain metabolic processes (Hussain et al. 2015) such as protein synthesis, and synthesis or repair of mitochondria, which permits the initial germination (Bray et al. 1989; Jisha et al. 2013; Paparella et al. 2015).

This chapter sums up the recent work accomplished on seed priming regarding its role in modulation of physio-biochemical and molecular mechanisms during germination and postgermination phases. It also discusses the basis of seed priming-induced enhancement of abiotic stress responses in crop plants during their different development stages.

2 Physiological, Biochemical, and Molecular Aspects of Seed Priming

2.1 Pregerminative Metabolism

At physiological level, priming treatments inflict various metabolic alterations in seed with the start of imbibition process (Bray et al. 1989; Bray 1995; Paparella et al. 2015). Because of rehydration in seed priming, major cellular processes in seed such as the de novo synthesis of proteins and nucleic acids, adenosine triphosphate (ATP) production, activation of antioxidants accumulation of phospholipids and sterols, and DNA repair mechanisms are regulated (Paparella et al. 2015). Seeds are commonly exposed to various abiotic stresses during the initial stage of their germination, and thus, the oxidative damage of nucleic acid, lipids, and proteins is not an unusual phenomenon (Kranner et al. 2010). Within this framework, the seed repair response is important for conserving seed vigor and efficient germination (Oge` et al. 2008). Proper repair of DNA damage allows the embryo cells to recommence cell cycle development and DNA replication occurs; nevertheless, oxidative injury because of defective DNA repair mechanisms leads to cell death (Kranner et al. 2010; Balestrazzi et al. 2011b; Waterworth et al. 2011; Ventura et al. 2012).

Priming treatments lead to an increased solubilization of storage proteins in seed, enhanced antioxidative activity (Bourgne et al. 2000; Randhir and Shetty 2005), and reduced lipid peroxidation rate in plants (Yeh et al. 2005). A proteome analysis of *Arabidopsis* seed germination after priming identified various storage proteins (12S-cruciferin β-subunits) which specifically appear during seed priming (hydro- and osmopriming) (Gallardo et al. 2004). Sung and Chang (1993) reported that other reserve mobilization enzymes such as isocitrate lyase (for mobilization of lipids) and carbohydrates (-amylases) are also triggered during seed-priming treatments. In primed seeds, a significantly higher number of mitochondria were also observed in osmoprimed leek cells (Corbineau et al. 2000). During priming treatments, upregulation of α- and β-tubulin subunits proteins, which are important in cell division, was also noted by Varier et al. (2010). Repair mechanism of DNA is an important constituent of the “pregerminative metabolism,” which is activated with the start of seed imbibition, accompanied by uncontrolled buildup of reactive oxygen species (ROS) (Paparella et al. 2015). Numerous studies have specified that the major DNA repair processes such as nucleotide- (NER) and base excision repair (BER) are stimulated during the early seed imbibition phase in order to sustain the genome integrity (Balestrazzi et al. 2012; Cordoba-Canero et al. 2014; Paparella et al. 2015).

The increased activities of antioxidant enzymes permit the control accumulation of ROS during water uptake by seed (imbibition process) (Bailly et al. 2000; Hsu et al. 2003). Scavenging ROS in seed is described as antioxidant potential of the seed, and essential requirement to enhance germination under environmental extremities (Liu et al. 2007). The antioxidative response of seed can be assessed by monitoring the expression profiles of genes encoding enzymatic antioxidant such as

SOD, which is important in scavenging of superoxide radicals (Yao et al. 2012; Paparella et al. 2015). Likewise, some other antioxidants such as CAT, APX, and GR were enhanced at transcript as well as enzyme activity level, representing the activation of antioxidant defense system (Chen et al. 2014; Macovei et al. 2014; Paparella et al. 2015). In short, seed priming activates various protective functions owing to physiological and metabolic alterations during pregerminative phase of seed, which provide the way for faster germination and vigorous seedling establishment.

2.2 *Better Imbibition and Vigorous Seedling Growth*

Seed priming may persuade structural and ultrastructural changes in seed that facilitates and speed up the process of imbibition, thus leading to uniform seedling emergence and better seedling stand establishment (Galhaut et al. 2014). The first phase of germination (imbibitions phase), which starts with the uptake of water by seed, is similar in both primed and nonprimed seed by comparing water uptake and time. During phase II (lag phase) of germination in primed seeds, hydration treatment permits controlled uptake of water by seed, whether alive or dead, and stimulates the pregerminative metabolic process, but emergence of radicle is prevented, characterized by the extended lag phase. Phase III (radical protrusion phase) is also similar in primed and nonprimed seeds and covers the germination and postgermination phases (Rajjou et al. 2012). Primed seed also showed the higher activities of many enzymes for metabolism of proteins (proteases), carbohydrates (α and β amylases), and lipids (isocitrate lyase) involved in mobilization of stored reserves in seed (Varier et al. 2010; Sisodia et al. 2018). These enzymes play pivot role in breakdown of the macromolecules for embryo growth and development that exerts positive influence on early and better seedling emergence (Varier et al. 2010). Seed priming can break seed dormancy, curtail seedling emergence time, improve seedling vigor, and leads to better germination and growth of plants (Mondal et al. 2011; Srivastava and Bose 2012). Seed priming with bioflavonoid enhanced both root and shoot elongation and increased the levels of photosynthetic pigments, flavonoids, and phenolics (Singh et al. 2016). Bose et al. (2018) stated that seed priming with polyethylene glycol significantly improved the levels of photosynthetic pigments under abiotic stress conditions.

2.3 *Osmotic Adjustment*

Seed priming has been reported to shorten the time of imbibition (phase I) and lag phases (phase II) (Khan et al. 2009; Ibrahim 2016). The embryo swelling inside the primed seed speeds up the germination process through facilitating the absorption of water (Elouaer and Hannachi 2012; Ibrahim 2016). Accumulation of osmolytes (e.g., sugars) is a crucial mechanism of plant stress tolerance (Ibrahim 2016), which reduces the osmotic potential (OP) of cell and allows osmotic adjustment (OA) under adverse environmental conditions (Matias et al. 2015; Kubala et al. 2015b; Ibrahim 2016). In priming, enhancement of physiological as well as biochemical changes takes place in seed during suspension of germination by negligible matric and low OP of the imbibing medium. Nonpenetrating organic solutes or salts in solid matrices (matriconditioning) and liquid medium (osmoconditioning) are used to generate the water potential equilibrium between seed and osmotic medium needed for conditioning. In *Vigna radiata* (mungbean), priming of seeds with sublethal dose of sodium chloride (halopriming) ameliorated the toxic effects of salinity stress by accumulation of osmolytes and enhancement of antioxidant defense system for OA (Saha et al. 2010). γ-Aminobutyric acid (GABA) treatment was helpful in maintaining an ideal OP in plants, which make them able to survive under osmotic stress conditions, without disturbing the normal functions of the cell. Lower OP with less change in leaf water content showed better OA while encountering osmotic stress (Hinckley et al. 1980). Higher proline (Pro) accumulation is also a common response of plants to osmotic stress (Ashraf and Foolad 2007). Proline regulates the cellular redox potential, stabilizes the macromolecules and subcellular structures, and triggers the stress-responsive genes/proteins (Szabados and Savouré 2010). During osmotic stress, accumulation of Pro occurs mainly due to reduced degradation and increased synthesis (Verbruggen and Hermans 2008), and partially occurs due to abscisic acid (ABA) and hydrogen peroxide (H_2O_2) signaling (Rejeb et al. 2014). While studying on *Zea mays* seedlings, Yang et al. (2009) demonstrated that the H_2O_2 led to Pro accumulation and upregulated the expression of Δ^1-pyrroline-5-carboxylate synthetase gene in radicle and coleoptile. Although accumulation of Pro has been reported in priming treated seeds (Farhoudi et al. 2011), little is known regarding the involvement of H_2O_2 and putative gene expression in this process.

2.4 Membrane Properties

Auto-oxidation of storage metabolites reserves during seed storage may lead to lipid peroxidation, which may further disrupt cellular compartmentalization and membranes (Rakshit and Singh 2018). Long-term storage of seed affects the activities and functions of various enzymes and cellular organelles, ultimately reducing the viability and vigor of seedling (Rakshit and Singh 2018). During seed priming, initial phase (phase I or imbibition phase) is characterized by repairing of mitochondria and DNA, enhanced respiration and energy metabolism, cell cycle initiation, hormone signaling, gene transcription and gene translation, and regulation of stress-responsive genes (DHN, LEA, AQP, etc.), activation of priming memory, ROS signaling, and regulation of antioxidant enzymes (Rakshit and Singh 2018). During lag phase, activation of priming memory and synthesis of protein through mRNA are recruited upon rehydration. In postgermination phase, mobilization of stored reserve and elongation of radicle cells occur, and after rupture of seed outer covering (seed coat), radicle emerges out (Chen and Arora 2013). Seed priming treatments trigger the active absorption of ions with higher ATP availability, and reduce the metabolites leakage via repair of deteriorated seed parts leading to improved growth of embryo (Dahal et al. 1990). Seed priming improves the cell membrane integrity, negates the oxidative damage, and counteracts lipid peroxidation, and these attributes are directly linked with repair of biochemical lesions (Villiers and Edgcumbe 1975), maintenance of seed viability (Basu et al. 1973), activation of enzymes (Sananda and Bose 2012), and improved rate of germination (Lee et al. 1998). It has also been reported that menadione sodium bisulfite, a novel priming agent (Prasad et al. 1994), was capable of inducing resistance against oxidative stress in *Arabidopsis* (Borges et al. 2009). Priming with polyamines has also been reported to stabilize the bilayer surface, retard the membrane deterioration (Basra et al. 1994), scavenge the free radicals, and protect the macromolecules and membranes from oxidative damages (Roberts et al. 1986; Besford et al. 1993) under adverse environmental conditions.

2.5 Antioxidant Defense System

In primed seedlings, different antioxidants such as POD, APX, SOD, and CAT have been known to play an important role in enhancing stress tolerance (Bolkhina et al. 2003). These antioxidants may guard the cellular membranes against the harmful effects of ROS such as H_2O_2, hydroxyl radicals, superoxide radicals, and singlet oxygen (Posmyk et al. 2001). Enhanced activities of CAT, SOD, and POD in seedlings emerged from primed seeds have been reported under normal and stress conditions (Goswami et al. 2013; Zheng et al. 2016; Hussain et al. 2016a, b).

Plant antioxidant systems scavenge the excessive ROS production persuaded by various stresses and play an important role during seed storage, germination, and development (Bailly 2004; De Tullio and Arrigoni 2003). Antioxidant system constitutes both enzymatic (such as APX, CAT, and SOD) and nonenzymatic compounds (e.g., GSH and AsA). Each antioxidant usually has a specific function, for instance, CAT degrades the H_2O_2 into water and oxygen, while APX-induced catalysis of H_2O_2 is reliant on AsA-GSH cycle. Here, AsA acts as election donor to stimulate H_2O_2 degradation by the APX, while GSH and its enzymes (monodehydroascorbate reductase; MDHAR, GR, dehydroascorbate reductase; DHAR) are accountable for AsA regeneration. Moreover, various antioxidants can have different functions at a similar developmental phase. For instance, CAT was regulated in dormant mature as well as germinating seeds, whereas APX was not noticed in physiologically quiescent seeds (De Tullio and Arrigoni 2003). Seed priming modifies the ROS accumulation and alters the expression of genes and enzymes of antioxidative defense system. Kibinza et al. (2011) noted that sunflower priming showed enhanced expression of gene encoding CAT and demonstrated that CAT is important enzyme that play role in recovery of vigor in the aged seeds.

2.6 Changes in Metabolic Events

Several metabolic events, such as DNA replication (Lanteri et al. 1994); synthesis of RNA, DNA, and proteins (Bray 1995; Bailly et al. 2000); and accumulation of beta-tubulin (De Castro et al. 1995), are triggered with seed priming (Paparella et al. 2015). In sunflower (*Helianthus annuus*), Chojnowski et al. (1997) noted that priming of seed increased the respiration rate and conversion of ACC (1-aminocyclopropane 1-carboxylic acid) to the ethylene. Understanding the responses of biochemical or molecular markers is of a significant interest for evaluating the efficacy of seed priming. In tomato (*Solanum lycopersicum*) seeds, a significant positive correlation was noted between DNA replication and osmotic treatment (osmoconditioning) (Bailly et al. 2000). Job et al. (1997) found that an 11-S globulin beta-chain was a good indicator among seed priming-induced effects in sugar beet (*Beta vulgaris*). Seed-priming treatments have been reported to improve the germination rate of aged seeds (Bailly et al. 1996, 2000), which was mainly attributed to lower lipid peroxidation rate, and restoration of antioxidative defense mechanisms, e.g., increased activities of GR and CAT (Bailly et al. 1996, 2000). The CAT enzyme controls the lipid peroxidation rate by scavenging of H_2O_2, while GR is known to produce glutathione.

Several other metabolic and cellular events such as including induction of stress-responsive proteins (LEAs and HSPs), cell division and elongation, H^+-ATPase activity, plasma membrane fluidity, and changes in proteome and transcriptome have been demonstrated to understand the basis of priming-induced abiotic stress tolerance in plants (Gallardo et al. 2001; Zhuo et al. 2009).

2.7 Hormonal Balance and Regulation

The antagonistic roles of different plant hormones like GA (gibberellin) and ABA in regulating seed germination are well understood (Bewley 1997). However, molecular and physiological mechanisms underlying the influence of seed priming treatments on germination in relation to plant hormones are poorly illustrated. The GA is crucial for seed germination, as evident by the inability of GA-deficient *Arabidopsis* (ga1-3) and tomato (gib-1) mutants to germinate without the exogenous application of GA (Groot and Karrssen 1987).

There are two distinct development programs involved in seed maturation and germination: shift from quiescent state to germination and switch from embryo development to maturation (Kermode 1990). Both steps are affected by the coordination between growth promoter (GA) and growth retardants (ABA) (Nambara et al. 2010). The interaction between ABA and GA is controlled by regulation of genes involved in signaling pathways and biosynthesis of these hormones and metabolism of germination-related proteins, stress proteins, and storage compounds (van der Geest 2002; Weiss and Ori 2007). Weitbrecht et al. (2011) have reviewed the role of ABA/GA in regulation of seed germination. During the embryogenesis, accumulation of ABA inhibits vivipary and modulates seed maturation. While GA antagonizes ABA during germination and development, therefore, GA biosynthesis signaling is generally reduced in mature seeds but increased during germination. El-Araby et al. (2006) reported that seed-priming treatments enhance GA/ABA ratio which, in turn, regulates seed germination. In primed seeds, the possible basis of regulation of hormones in relation to germination includes different GA-induced germination-related processes, mainly including weakening of endosperm, reserve mobilization, and elongation of embryo cell (Chen et al. 2001; Chen and Bradford 2000; Nonogaki et al. 2000; Chen et al. 2002; Sung et al. 2008). Only few studies exist on interaction of ABA and GA during seed priming, and its contribution in seed priming-induced regulation of germination. The available studies have outlined a differential response of seed priming (e.g., increased ABA signaling during seed priming) to ABA-GA interaction (Lopez-Molina et al. 2002; Catusse et al. 2011).

Ethylene also affects the germination process through enhancing speed and rate of germination (Siriwitayawan et al. 2003). The relationship between priming and ethylene has been reported in various plant species, such as peanut, cucumber, tomato, and lettuce (Cantliffe et al. 2000; Habdas et al. 1998; Siriwitayawan et al. 2003). Two different mechanisms are suggested regarding the role of ethylene in seed priming: (1) higher ethylene production enhances the activity of endo-β-mannanase, which can help germination at high temperature via weakening of endosperm, and (2) ethylene can modulate OA by regulating the osmotic adjustment in primed seeds and increasing germination even under stressful conditions (Cantliffe et al. 2000).

2.8 Aquaporins and Tonoplast Intrinsic Proteins

Aquaporins (AQPs) have significant role in kinetic exchange of water. Recently, different studies have demonstrated the better water uptake in primed seeds because of faster imbibition with respect to nonprimed seeds (Galhaut et al. 2014; Kubala et al. 2015a), and the ectopic expression of AQPs genes (SoPIP2; 1) was enhanced in primed seeds (Chen et al. 2013). The transmembrane transport of water through the regulation of AQPs enhanced the capacity of seed to absorb and transport water to different plant tissues. It was observed that during imbibition process, the transport of water and adequate water supply for the embryo through AQPs might be one of the major components mediated in primed seeds, that impacts the rate of germination as well as stress resistance (Chen et al. 2013; Wojtyla et al. 2016).

Increased germination potential and vigor of seeds under different priming techniques have been well reported (Hu et al. 2005; Pant and Bose 2016). In *Arabidopsis* model plant, proteomic analysis in primed and unprimed seeds identified 1300 proteins, and an abundant change was recorded in 74 proteins prior to emergence, and some new proteins were identified during dehydration (Gallardo et al. 2001). In wheat seeds, proteomics analysis during artificial aging and seed priming (hydropriming) showed 162 differentially expressed proteins (DEPs) responsible for energy supply, metabolism, and stress responses (Lv et al. 2016), while 531 DEPs were noted in primed seeds compared to nonprimed seeds, and various upregulated DEPs are involved in process of energy supply (such as tricarboxylic acid cycle, glycolysis, fatty acid oxidation), anabolic processes (such as synthesis of various fats and amino acids), and cell division and growth (Lv et al. 2016).

2.9 Dehydrins (Late Embryogenesis Abundant Proteins)

DHNs (group 2 LEA protein) (Candat et al. 2014) are associated with enhanced stress tolerance in primed seeds (Wechsberg et al. 1994). Degradation of DHN was noted during priming (osmopriming) in *Pisum sativum* L. (peas) and *Beta vulgaris* L. (beet) (Capron et al. 2000; Baker et al. 1995; Gumilevskaya and Azarkovich 2010), indicating that primed seeds may reduce DHNs than unprimed seeds. A reduction in the abundance of DHNs in primed seeds was noted in *Pisum sativum* (peas), *Spinacia oleracea* (spinach), and *Beta vulgaris* (beet) compared to unprimed seeds (Baker et al. 1995; Chen et al. 2012a, b). Chen et al. (2012b) found four DHN-like proteins in spinach seeds during early phase of osmopriming and they demonstrated that these proteins were degraded progressively to a lower level in primed seeds, compared with untreated seeds.

2.10 Reactive Oxygen Species: Key Signaling Molecules in Priming

Seed priming alters the accumulation of ROS in plants (Pal et al. 2013). Several evidence indicate that ROS, although toxic at higher concentration, could also assist as signal molecules to regulate hormone signaling, programmed cell death, plant growth and development, and tolerance against various abiotic stress factors (Mittler et al. 2004). ROS also contribute in sensing of the external environment and thus control the plant development (Smirnoff 2005). A complex system is present for ROS metabolism that interacts closely with hormonal signaling systems and assists plants in regulation of developmental proceedings as well as abiotic stress responses (El-Maarouf-Bouteau and Bailly 2008). These authors noted that light or moderate accumulation of ROS is beneficial for germination, as it may activate signaling cascades for seed germination, promote the weakening of endosperm, and mediate programmed cell death in the aleurone layer (Bailly et al. 2008; El-Maarouf-Bouteau and Bailly 2008). Under priming treatments, such beneficial accumulation of ROS may occur from partial hydration and dehydration of seed. Bailly et al.

(2008) reported the decreased ROS accumulation during seed development of in sunflower; however, their levels were increased rapidly with seed hydration because of regulation of various ROS-producing metabolisms mainly including lipid catabolism and respiration. During seed-priming process, the enhanced ROS production can be a natural response that occurred due to the partial hydration of seed, rather than an indicator of stress. Nevertheless, H_2O_2 accumulation was enhanced by PEG exposure (>24 h) in *Medicago* (Balestrazzi et al. 2011a). Likewise, a combined application of GA and PEG persuaded high accumulation of ROS in *Larix deciduas* (Larch) and *Pinus sylvestris* (pine) seeds (Naglreiter et al. 2005). Apart from the positive role of ROS, an excessive generation of ROS can be injurious to germination of seed because these may cause seed aging and cellular perturbations (McDonald 1999). It was suggested that the accumulation of ROS should be controlled tightly in order to play the role of positive regulator of germination (Bailly et al. 2008), particularly during osmopriming where less availability of the water can cause more production of ROS.

2.11 Activation of DNA Repair Pathways

DNA repair and defense mechanisms are stimulated in seeds upon rehydration to decrease the growth inhibition during development of seedling. During maturation and storage conditions, seeds are exposed to various adverse conditions, which cause DNA oxidation, loss of D NA integrity, and hinder the cell cycle (Bray and West 2005). To increase the chances of successful germination and preserve the seed vigor, DNA repair processes must be kept at proper level in embryo. DNA repair mechanisms mainly including BER and NER together with antioxidants are regarded as key pregerminative metabolic processes (Huang et al. 2007; Wojtyla et al. 2016). In barrel clover (*Medicago truncatula*) seeds, the TYROSYL-DNA PHOSPHODIESTERASE (MtTdp1α; GB# FJ858738) and MtTdp1β (GB# BT006446.1) genes encoding α- and β-tyrosyl-DNA phosphodiesterase1 and DNA repair genes MtTop1α (GB# CA919655) and MtTop1β (GB# CX526330) were upregulated rapidly during the imbibition process (Macovei et al. 2010; Wojtyla et al. 2016). The increased expressions of MtTop1 α and MtTop1 β and as well as for MtTdp1 α and MtTdp1 β were also noted during PEG priming of *Medicago truncatula* seeds (Balestrazzi et al. 2011a). In *Arabidopsis* seed, enhanced expression of AtOGG1 gene (DNA glycosylase) was also recorded during desiccation and water uptake (Wojtyla et al. 2016). The PEG priming of *M. truncatula* seeds also showed the involvement of AtTFIIS and MtTFIIS in DNA repair mechanisms during seed imbibition (Macovei et al. 2011b; Wojtyla et al. 2016), but Balestrazzi et al. (2011a) demonstrated that higher regulation of TFII-S was not observed in PEG-primed seeds. DNA repair mechanisms (NER, BER, HR, etc.) are now regarded as pregerminative metabolic process, important for recrudescence of cell cycle activity (Huang et al. 2007; Wojtyla et al. 2016). The repair processes of DNA should be regarded as the most valuable and essential process activated in the process of seed priming (Macovei et al. 2011a; Ventura et al. 2012; Rajjou et al. 2012). Prior to replication in primed seeds, repair of DNA damage occurs primarily through DNA synthesis (Varier et al. 2010). In chick pea seeds, the role of DNA repair during seed priming was suggested based on the expression analysis of genes involved in DNA repair directly or indirectly (Sharma and Maheshwari 2015; Wojtyla et al. 2016). Seed priming also regulates the expression of some genes/proteins which play essential role for cell division. In *Arabidopsis thaliana* seeds, both osmoprimed (−0.75 MPa PEG 6000) and hydroprimed resulted in accumulation of tubulin subunits (α tubulin and β tubulin) (Gallardo et al. 2001; Kubala et al. 2015a). In osmoprimed seeds of *Lycopersicon esculentum*, DNA replication and synchronization of cell cycle were also recorded (Özbingöl et al. 1999; Wojtyla et al. 2016). Moreover, osmopriming (1.2 MPa PEG) in *Brassica napus* seeds enhanced the regulation of genes/proteins involved in cell cycle, such as microtubule motor activity proteins (At3g45850, At4g39050), proteins associated with microtubule (At5g55230, At1g24764), cell division control protein 48 homolog C (At3g01610; CDC48C), and tubulin subunits (beta- and gamma-tubulin) (Kubala et al. 2015a; Wojtyla et al. 2016). The above discussion partially confirmed that different priming techniques promote higher and faster activation of pregerminative metabolism, such as DNA processing during replication and repair mechanisms, and transcriptional activity.

3 Seed Priming and Abiotic Stress Tolerance in Plants

Crop plants often pass through a period of abiotic stresses during their life cycle under natural environments which adversely affect their growth and productivity (Hussain et al. 2018a). Different stresses such as drought, heat, cold, and salinity are threatening the crop yields. To counter the effects of these abiotic stresses, plants modulate various physio-biochemical processes. It has been well understood that most of the abiotic stresses decrease the uptake during first phase of germination. Less water availability under abiotic stresses affects the process of the cell elongation, leading to reduced embryo growth followed by poor emergence of seedling. Seed priming, a pragmatic technique, has been successfully employed to achieve the proper stand establishment under normal and stressful conditions (Jafar et al. 2012; Hussain et al. 2016a, b). Recently, several reports have described the beneficial impacts of priming under different abiotic stresses in various field crops (Jisha et al. 2013; Hussain et al. 2016a, b; Hussain et al. 2018a). Plants emerged from the primed seeds showed vigorous head start and higher stress tolerance mainly because of more effective energy metabolism, OA, quick cellular defense systems, enlarged embryo, and enhanced enzymatic activation (Jisha et al. 2013). In PEG-primed seeds, Pant and Bose (2016) noted that the germination, vigor, and relative water content were enhanced with respect to nonprimed seeds. Under cold stress, seed priming with salicylic acid (SA) + H_2O_2 combination significantly enhanced germination and seedling growth, which was closely related with ROS detoxification, hormonal metabolism, metabolites accumulation, and efficient energy supply (Li et al. 2017). In tobacco, seed priming enhanced the cold tolerance during germination and growth of seedling by regulation of antioxidative defense in plant tissues (Xu et al. 2011). Guan et al. (2009) demonstrated that seed priming improved the germination speed and seedling growth of maize under low temperature. Similarly, Elkoca et al. (2007) suggested the seed priming (hydropriming and osmopriming) for better seedling emergence and vigorous growth of chickpea under chilling stress. Srivastava et al. (2010) reported the beneficial influence of various seed-priming techniques to increase salinity and drought tolerance in Indian mustard. Kumar et al. (2016) stated that hydro- and halopriming ($Mg(NO_3)_2$ and $Ca(NO_3)_2$) can alleviate the adversities of heavy metal ($HgCl_2$) stress in wheat by enhancing the germination, seedling length, soluble sugar contents, and α amylase activity.

4 Conclusion

Seed priming offers a smart, innovative, realistic, and effective option for achieving faster and uniform emergence, vigorous stand establishment, and higher productivity in crop plants under normal and stressful conditions. Vigorous start and greater stress tolerance in plants raised from primed seeds primarily occur because of more effective energy metabolism, OA, embryo enlargement, enhanced activation of different enzymes, increased DNA and RNA synthesis, and quick cellular defense responses. Seed priming can stimulate various signaling cascades during early growth phase and leads to faster and efficient defense responses in plants. The exact molecular mechanisms behind seed priming are not fully explored; it is postulated that sensitization of seed was related with higher buildup of signaling proteins. Under abiotic stress conditions, activation of signaling proteins amplifies signal transduction, thus resulting in rapid activation of plant defense responses. Priming helps repair some of the damages caused by seed erosion, which leads to increased vigor of primed seeds. Seed priming also affects the metabolic phase of germination and thus triggers the early replication of DNA. It is desirable to develop the appropriate seed-priming approaches for different plant species to overcome the challenges of the environmental extremities. Although the beneficial effects of seed priming in enhancing abiotic stress tolerance in plants are widely reported, the exact mechanism behind such effects is poorly known. Therefore, the imminent goals of agricultural researchers should be focused on identifying the novel proteins/genes and transcription factors, which are regulated due to seed priming under different abiotic stresses.

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