Seed Osmolyte Priming and Abiotic Stress Tolerance

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1 Introduction

Seed priming is any technique in which seeds are imbibed in a solution prior to sowing in order to improve germination rates and uniformity and/or to confer abiotic and biotic stress tolerance. Priming can be performed with water alone (hydropriming) or with chemical or bioactive compounds (Paparella et al. 2015). The controlled seed rehydration induced by priming triggers metabolic processes associated with early states of germination such as restoration of cellular integrity, initiation of respiration and DNA repair functions, and increased activity of antioxidant enzymes and reactive oxygen species (ROS) scavenging. Priming with water, chemical, or biological solutions can enhance seedling or mature-plant tolerance to abiotic stresses.

The method of introducing a priming compound into a seed (soaking, solid matrix priming, seed coating) can influence the efficacy of the treatment (Klein et al. 2017; Wang et al. 2016). Priming conditions – chemical concentrations/osmotic potentials, durations, and temperatures – can in turn affect the amount of material taken up by the seed (El-Araby and Hegazi 2004; Posmyk et al. 2008). With the correct priming conditions, a seed has a high enough water content to initiate germination-related processes, but low enough to prevent germination (radicle emergence) and to retain desiccation tolerance upon drying. The specific processes induced by priming and the degree of their expression may also vary depending on plant species, seed structure, and quality (Paparella et al. 2015). Embryo location (external as in monocots or internal as in dicots) may influence the ability of a priming compound to affect seed germination and seedling growth, as can amount of endosperm (low in onions or tomatoes versus high in wheat or beans). The amount of mucilage generated on the seed coat (as in basil or rocket seeds) may also affect uptake and effectiveness of the priming compounds (Western 2012, and references therein).

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We review here recent and foundational literature on methods and compounds used in seed priming to achieve tolerance to abiotic stress in emerging and growing plants, as well as proposed mechanisms of action and potential for future research and development.

2 Abiotic Stress in Plants: Phenomenon and Induced Tolerance

Abiotic stress can affect all major aspects of plant development, from seed germination to growth, flowering, and seed development. The degree to which a given stress affects a crop depends both on the severity and on the crop's tolerance or resistance to the stress. The effects of abiotic stress, and the plant's responses, are specific to the type of stress (i.e., limited photosynthesis and nutrient availability under drought and salinity, suboptimal cellular respiration under heavy metal stress, and slowed metabolic activity in cold temperatures). Under all abiotic stresses, though, plants produce toxic levels of ROS capable of lipid peroxidation, protein denaturation, and DNA mutation (Jaspers and Kangasjärvi 2010). Although necessary for proper development at low concentrations, ROS concentrations accumulate to toxic levels under abiotic stress and become particularly damaging to organelles such as mitochondria and chloroplasts, which facilitate a high rate of electron flow (Gill and Tuteja 2010). A common response to abiotic stress is therefore the induction of antioxidative enzymes and metabolites to neutralize the damaging effects of ROS (Bernstein et al. 2010). The specific antioxidant compounds (enzymatic and nonenzymatic) upregulated during stress conditions and the degree of their expression are influenced by the plant developmental state, duration of stress, and subcellular localization of ROS accumulation (Reddy et al. 2004; Gill and Tuteja 2010).

Another general characteristic of stress tolerance is maintaining osmotic homeostasis, which is critical for protecting membranes from desiccation and facilitating continued nutrient uptake from a potentially high-ionic root zone, such as during salinity or heavy metal stress. Maintaining osmotic homeostasis is achieved in general by increasing the concentration of osmolytic compounds, for example, total soluble sugars (Jisha and Puthur 2016b), and/or amino acids such as proline (Hayat et al. 2012).

Abiotic stress tolerance is a complex biological trait expressed both physiologically and morphologically through altered gene expression, modified hormone levels, metabolite biosynthesis, and antioxidant activity (Zhang et al. 2014; Nguyen et al. 2018). Examples of stress tolerance responses include increasing root growth, modifying cellular relative water content via osmotic adjustment, and abscisic acid-induced stomatal closure to improve water use efficiency upon drought and salinity stress (Bartels and Sunkar 2005; Taiz and Zeiger 2006), and faster and more efficient utilization of storage compounds during chilling stress (Hussain et al. 2017).

3 Priming Compounds Conferring Abiotic Stress Tolerance in Plants

Plant growth regulators (PGRs) are naturally occurring or synthetic compounds which modify developmental and/or metabolic processes by specifically affecting a plant's natural hormone system (Rademacher 2015). Often bioactive at very small concentrations, PGRs are widely used to modify plant morphology, confer stress tolerance, improve yield, and increase harvesting efficiencies. In addition to the bioactive compound used, the method of PGR application and plant developmental stage is critical to achieve the desired effects.

Under abiotic stress conditions, exogenous application of PGRs induces common stress tolerance responses such as increased antioxidant enzyme activity, leaf proline content, and relative water content. Examples include the brassinosteroid 28-homobrassinolide on Indian mustard (*Brassica juncea*) (Zhang et al. 2014), melatonin on fava beans (*Vicia faba*) (Dawood and El-Awadi 2015), salicylic acid on rice (*Oryza sativa*) (Wang et al. 2016), and gamma aminobutyric acid (GABA) on ryegrass (*Lolium perenne*) (Krishnan et al. 2013).

While PGRs are usually applied as a foliar spray, they have proven to be valuable seed priming agents as well. Wheat seeds (*Triticum aestivum*) primed with benzyl aminopurine had increased α-amylase activity and soluble sugar concentrations during salt stress (Bajwa et al. 2018). Under drought conditions, rice grown from seeds primed with salicylic acid had increased antioxidant activity, osmolyte concentration, and cellular water potential (Farooq et al. 2009). Red cabbage seedlings (*Brassica oleracea rubrum*) grown from melatonin-primed seeds had higher germination rates, decreased levels of lipid peroxidation, and higher fresh weight when grown under high concentrations of copper (Posmyk et al. 2008).

In addition to traditional PGRs, essential oils (EOs) and botanical extracts are increasingly used in place of synthetic compounds to protect against biotic and abiotic stresses. Thymol and carvacrol, monoterpenes derived from the essential oils of thyme and oregano, have antioxidant properties which support membrane integrity during abiotic or biotic stresses (De Azeredo et al. 2011; Ye et al. 2016). Seedlings grown from radish seeds (*Raphanus raphanistrum*) imbibed in carvacrol had increased pigment (carotenoid and anthocyanin) concentrations, antioxidant activity, and survival rate under drought conditions (Klein et al. 2017). Thymol-priming reduced the effects of salinity stress on pea seedlings (*Pisum sativum*) by increasing superoxide dismutase (SOD) activity (Kazemi 2013). Rice seeds primed with sunflower extract had increased root and shoot length and increased fresh weight when grown under high salinity (Farooq et al. 2011). Allelopathic sorghum extract priming increased total phenolics and soluble sugar concentrations and decreased Na^+ content in wheat grown under high salinity (Bajwa et al. 2018).

Given their bioactivity at small concentrations, optimal priming concentrations for PGRs, EOs, and botanical extracts need to be determined to avoid negatively affecting germination and seedling development (Fariduddin et al. 2003; Posmyk et al. 2008; Martino et al. 2010; Arteca 2013). Recently, priming with osmolytic compounds has received considerable interest by the scientific community. Some of the beneficial effects of priming with osmolytic compounds in various plant species against different abiotic stresses and at various stages of plant growth are shown in Table 1.

Table 1 Selected references for seed priming with osmolytes and resulting abiotic stress tolerance

Priming compound	Plant species	Concentration and duration of priming	Positive effects of priming regulating stress tolerance	Reference
Proline	*Vigna radiata*	5 mM and 150 mM proline; 6 hours	Increased germination %, proline content, and hypocotyl growth, decreased lipid peroxidation under chilling stress	Posmyk and Janas (2007)
	Oryza sativa L.	1, 5, and 10 mM proline; 12 hours	Increased root and shoot length, chlorophyll concentration, and proline biosynthesis under salinity stress	Deivanai et al. (2011)
Mannitol	*Cakile maritima* L.	2% mannitol solution; 12 hours	Increased RWC, GSH and proline content, and SOD activity, decreased MDA levels under drought and salinity stresses	Ellouzi et al. (2017)
	Medicago sativa L.	4% mannitol; 12 hours	Increased root and shoot length, proline content, and antioxidant activity, decreased ion leakage under salinity stress	Amooaghaie (2011)
	Cicer arietinum L.	1–10% mannitol; 24, 48, 72 hours	Increased root and root fresh and dry weight, amylase and sucrose synthase activities, and total leaf sugar content under osmotic stress	Kaur et al. (2005)
Glycinebetaine (GB)	Four turfgrass species	50, 100, 150, and 200 mM GB; 24 hours	Increased germination rate, seedling fresh weight, and water content under both osmotic and salinity stresses	Zhang and Rue (2012)
	Oryza sativa L.	50, 100, and 150 mg/L GB; 48 hours	Increased leaf GB content, soluble sugar and antioxidant concentrations, increased RWC, and decreased ion leakage under drought stress	Farooq et al. (2008)
Trehalose	*Zea mays* L.	10 mM trehalose; 8 hours	Decreased ion leakage and lipid peroxidation, increased leaf K/Na ratio under salinity stress	Zeid (2009)
	Raphanus sativus L.	25 and 50 mM trehalose; 14 hours	Increased root fresh weight, GB content, antioxidant content and activity, decreased lipid peroxidation under drought stress	Shafiq et al. (2015)

(continued)

Table 1 (continued)

Priming compound	Plant species	Concentration and duration of priming	Positive effects of priming regulating stress tolerance	Reference
Spermidine	*Oryza sativa* L.	5 mM spermidine; 24 hours	Increased phenolic, GB, soluble sugar and protein contents, α-amylase, and antioxidant activities under chilling stress	Sheteiwy et al. (2017)
	Triticum aestivum L.	5 mM spermidine; 12 hours	Increased stomatal conductance and grain yield, decreased shoot [Na^+] and [Cl^-] under salinity stress	Iqbal and Ashraf (2005)
	Trifolium repens	30 μM spermidine; 3 hours	Increased α-amylase activity, fructose and glucose concentrations, increased antioxidant activity, and decreased lipid peroxidation under osmotic stress	Li et al. (2014)
GABA/BABA	*Trifolium repens*	1 μM GABA; 2 hours	Increased root and shoot length, fresh and dry weight, and dehydrin concentrations, decreased peroxidation levels under salinity stress	Cheng et al. (2018)
	Oryza sativa L.	0–2.5 mM BABA; 12 hours	Increased pigment concentration, PS I and II activities, antioxidant enzyme activity, and proline content, decreased MDA concentration under salinity and osmotic stresses	Jisha and Puthur (2016b)

4 Possible Mechanisms of Osmolyte Priming: Induced Abiotic Stress Tolerance

The currently understood mechanisms of priming for abiotic stress tolerance are twofold. Seed imbibition and drying promote the seed to an advanced germinative state such that primed seeds germinate faster and at higher rates than non-primed seeds under adverse conditions, resulting in increased competitiveness for limited resources and overall yield increases (Chen and Arora 2013; Paparella et al. 2015). This advanced germinative state is the result of multiple induced processes such as repair and increased synthesis of metabolic machinery, cell-cycle components, aquaporin activity, and ion transporters. Seed imbibition additionally promotes increased gibberellic acid (GA) biosynthesis and abscisic acid (ABA) degradation, thus furthering the germinative state via reserve mobilization and endosperm weakening (Bewley et al. 2012; Chen and Arora 2013; Zhang et al. 2014).

Seed imbibition with water alone also imparts a stress imprint or “memory” to the seed which remains after drying. Even under optimal priming conditions, and regardless of the protocol used, seed hydration and drying are inevitably damaging to a seed due to ROS production and membrane disruption upon imbibition and the likely decreased desiccation tolerance caused by drying (Chen and Arora 2013). Improper priming conditions, such as rapid water uptake, priming at low temperatures, and/or rapid drying, would therefore only exacerbate such damage (Bewley et al. 2012).

This stress imprint is often connected to increased antioxidant activity and protective compounds in the seedling. Antioxidant enzyme activity has been correlated to stress tolerance in many plant species (Munns 2002; Ashraf and Ali 2008; Posmyk et al. 2008; Zhang et al. 2014; Hussain et al. 2017). Increased antioxidant activity can be attributed both to seed rehydration in general and to specific priming agents and conditions to induce stress (osmotic, salinity, heavy metal, etc.) such as seed microencapsulation (Murungu et al. 2004) or priming temperature and duration (Bujalski and Nienow 1991). Based on their bioactivity and concentration, the specific priming compounds used may further influence seed germination and seedling growth beyond that of water alone (hydropriming) (Posmyk et al. 2008; Baier et al. 2019; Bajwa et al. 2018).

The protective effects of seed priming against oxidative stress have been extensively reported. Primed seedlings exposed to abiotic stress had increased activities of ROS scavenging enzymes such as superoxide dismutase, catalase, and ascorbate peroxidase (Bailly et al. 2000; El-Araby and Hegazi 2004; Lei et al. 2005; Hussain et al. 2017; Latif et al. 2016). In all cases, seedlings from primed seeds had higher germination rates and decreased levels of lipid peroxidation. Priming also combats oxidative stress by increasing polyphenol and pigment biosynthesis (Bailly 2004; Nouman et al. 2012; Latif et al. 2016; Klein et al. 2017).

In addition to increasing ROS scavenging, seed priming with osmolytes directly supports membrane integrity and protein structure during abiotic stress. This has been achieved by increasing the concentration of late embryogenesis abundant (LEA) proteins in polyethylene-glycol (PEG)-primed pepper (Cortez-Baheza et al. 2007), heat shock proteins in hydroprimed sugar beet (Catusse et al. 2011), and protein folding and stabilization proteins in PEG-primed rapeseed (Kubala et al. 2015).

The ability of plants to break down starch into an adequate supply of soluble sugars for metabolism is crucial for survival and tolerance to abiotic stresses (Rosa et al. 2009; Zheng et al. 2016). Rice seedlings from KCl and $CaCl_2$ primed seeds demonstrated increased starch hydrolysis and resulted in greater yield (Farooq et al. 2006). Under salinity stress, BABA-primed mung bean seedlings had increased soluble carbohydrate levels, contributing to increased photosynthetic pigment concentration and seedling fresh weight (Jisha and Puthur 2016a).

An additional benefit of increased soluble sugar concentrations is to support cellular osmotic homeostasis (Jisha and Puthur 2016a), which, as previously noted, supports nutrient uptake and membrane integrity. Priming-induced mechanisms to increase osmolyte concentrations also include increasing proline, as noted in cauliflower (Latif et al. 2016), and total soluble protein concentrations in wheat (Bajwa et al. 2018).

5 Conclusion and Future Perspectives

The beneficial effects of seed priming have not been observed consistently. Most studies to date do not report beneficial residual effects of seed priming beyond the seedling stage or without early stress exposure. Protection induced by priming is often more pronounced if the stress is present at sowing, upon germination or shortly after emergence.

Certain priming treatments are species-specific, perhaps based on the structure of the seeds and the amount of endosperm they contain that can “store” the priming compound (Dawood 2018; Zheng et al. 2016). The protective effects of a priming treatment, if expressed at all, do not always persist as the plant matures or if it grows in nonstressed conditions (Cayuela et al. 1996; Posmyk et al. 2008; Poonam et al. 2013; Jisha and Puthur 2016a; Savvides et al. 2016; Ye et al. 2016; Ellouzi et al. 2017). Some studies have reported a beneficial residual effect of seed priming beyond the seedling stage and/or without the immediate induction of stress such as maize seeds soaked in water (Murungu et al. 2004), or microencapsulated with the fungicide tebuconazole (Yang et al. 2014), and melatonin-primed fava beans (Dawood and El-Awadi 2015). Although epigenetics have been invoked as a possible mode of action for the protection provided by seed priming (Savvides et al. 2016), there is not yet evidence that plants that grow from primed seeds can themselves produce seeds with endogenous protection.

There is no evidence that any of the osmolytes or other compounds thus far studied as priming materials are injurious to human health or to the environment at the concentrations used with seed treatments. However, fungal and bacterial populations on seeds can increase during extended treatment with osmolytes (Wright et al. 2003), even if the seeds are subsequently coated with antimicrobial compounds, but this is unlikely to affect human health in seeds that germinate. In extreme cases, ingesting plants with an induced overproduction of natural antioxidants can cause internal injury (Bast and Haenen 2002), although this is unlikely to occur as a result of seed priming. However, there is evidence that antioxidant activity measured in vitro may not correlate with the actual activity in vivo (Ndhlala et al. 2010). Noninvasive methods of measuring both plant structures (Tardieu et al. 2017) and physiological compounds or mechanisms (Boughton et al. 2016) which protect against abiotic stress must be further developed to allow in vivo measurement of the effects of priming treatments. This will provide both more accurate measurements of the true influence of seed treatments and may well provide an impetus to the development/discovery of more and better-targeted osmolytes and other compounds. The resulting improved plant resistance to abiotic stress will in turn enhance food security in an era of global uncertainty.

We suggest three fronts for further investigations of seed priming for abiotic stress resistance:

1. Growing plants from treated seeds to maturity, so as to ensure that there are no negative effects of treatments on quality or yield, despite the fact that the seedling can withstand stress.

2. Developing treatments with effects that persist if treated seeds are stored for one or more seasons after treatment.
3. Always testing seeds from at least two cultivars of the plant being investigated, to ensure that the treatment being developed will be suitable for as broad a genetic background as possible.

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