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On-farm seed priming interventions in agronomic crops

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ABSTRACT

Priming techniques are gaining importance in agriculture with the increase in environmental stresses. Resource-poor farmers are in urgent need of such techniques as they are simple, economical, and value-added intervention associated with low-risk bearing factors. Seed enhancement methods are key to improve seed performance and achieve a good stand establishment. Worldwide beneficial effects of priming are recorded. But these technologies have still not reached most farmers. This review highlights the importance of on-farm priming strategies in modern crop production system to yield better productivity and obtain higher economic returns. Stimulation of the pre-germination metabolic changes by priming is necessary to overcome the environmental challenges that a plant can encounter. Thus, the study also focuses on mechanisms associated with priming-induced stress tolerance of crops. Various safe practical methods of seed priming can be easily adopted by the farming community to alleviate the levels of different stresses which can hamper productivity. Simultaneously they can produce good quality seeds and use them further for the next crop cycle cutting the costs of seed purchase.

Key words: priming methods; priming agents; stress; stress tolerance; plant growth

IZVLEČEK

UVAJANJE PREDSETVENE OBDELAVE SEMEN POLJŠČIN NA KMETIJAH

Tehnike predsetvene obdelave semen pridobivajo na pomenu v kmetijstvu s povečevanjem okoljskih stresov. Zaradi preprostosti uporabe, ekonomičnosti in dodane vrednosti zaradi zmanjšanja tveganja so te metode nujno potrebne za revne kmete. Metode pospeševanja kalitve semen so ključne za izboljšanje setve in za vzpostavitev dobrih posevkov. Blagodejni učinki predsetvene obdelave semen so zabeleženi širom po svetu, vendar te tehnologije še vedno niso dosegle večine kmetov. Ta pregled osvetljuje pomen teh postopkov na kmetijah v modernih sistemih pridelovanja poljščin za boljšo produktivnost in doseganje večjih iztržkov. Vzpodbujanje predkalitvene presnovne aktivnosti semen z njihovo predsetveno obdelavo je potrebno za preseganje okoljskih izzivov s katerimi se soočajo rastline. Raziskava se osredotoča tudi na mehanizme, povezane s predsetveno obdelavo semen vzpodbujene tolerance na stres pri kmetijskih rastlinah. Različne varne in praktične metode predsetvene obdelave semen bi lahko bile z lahkoto uporabljene pri kmetovalcih za zmanjševanje okoljskih stresov, ki ovirajo produktivnost rastlin. Hkrati bi tako pridelali kvalitetna semena za naslednjo setev in s tem zmanjšali stroške njihovega nakupa.

Ključne besede: metode predsetvene obdelave semen; sredstva za predsetveno obdelavo; stres; toleranca na stres; rast rastlin

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1 INTRODUCTION

Farmers in developing countries often encounter poor crop establishment in crop production practices. The reasons for this failure might be due to some basic factors like availability of good quality seeds, knowledge of seed technology, proper sowing techniques, or climate change and various environmental stresses (Figure 1). The extra costs in labour, draft power, and materials hinder the small and marginal farmers to alleviate these constraints efficiently. Therefore, we need to popularize the seed enhancement technologies which could be easily adopted by all farmers, irrespective of their socio-economic conditions. Because successful crop production depends on good quality seeds.

Abiotic and biotic stresses are the norm for any plant while completing its phenology (Suzuki et al., 2014). Among others, the predominant abiotic stresses include extremes of temperature, drought, high salinity, nutrient, and oxidative stress. While pathogens (fungi, bacteria, viruses, and nematodes) and pests (insects, arachnids, herbivores, and weeds) are threats to plants as biotic stress. These stresses are known to cause physiological, biochemical, and metabolic changes in crop plants affecting the metabolism, performance, and ultimately adversely reducing the yield of plants (Anjum et al., 2011; Rejeb et al., 2014).

High salt stress is the cause for disruption of water relations and ionic distribution in plants (Munns & Tester, 2008). Basically, salinity has a negative impact on seed germination and seedling establishment either by inhibiting water uptake with development of high external osmotic potential or through accumulation of toxic ions (Na^+ and Cl^-) in the system (Nasri et al., 2015; Negrão et al., 2017). Water is a primary factor of production, and hence drought stress, particularly at the critical growth stages is one of the major environmental limiting factor affecting crop growth and productivity (Araus et al., 2002). The negative consequences of drought stress can be seen in every aspect of plant life (Rahman et al., 2004). Drought stress is known to bring about a series of adverse effect in biochemical and physiological processes of plants, viz., disturbance in ion homeostasis and enzymatic activities, increased levels of reactive oxygen species (ROS), decreased cell division, leaf parameters (area, size, and chlorophyll contents), CO_2 assimilation, photosynthesis, root proliferation, stem elongation, and water use efficiency, and consequently reduction in grain yield (Farooq et al., 2009; Anjum et al., 2011; Farooq et al., 2012; Nikju et al., 2015). Moreover, seeds sown in dry soil often delays in germination as they absorb too little water from the soil, following delay in several imbibition processes. If a method of germination could be devised to overcome with this time lag in germination by pre-soaking of the seeds in water, germination would occur swiftly ensuing in a better crop stand.

Another major global constraint in productivity of agricultural crops is the inaccessibility of nutrients by plants due to their deficiency in soil, commonly known as nutrient stress (Baligar et al., 2001; Sun et al., 2011). Both macro- and micronutrients have great roles in meeting crops demands and improving the yield levels. Micronutrient deficiency has already been found in the food chain; proper management strategies focusing on nutritional quality is a serious concern in sustainable agriculture (Khoshgoftarmanesh et al., 2010). Several other abiotic stresses like cold, heat, light, or irradiation can adversely alter the plant physiology and govern the occurrence of biotic stresses in the environment (Suzuki et al., 2014; Pandey et al., 2017).

Plants in response to multiple environmental stresses activate various defense mechanisms and signaling pathways regulated by ROS, hormones (salicylic acid, abscisic acid, jasmonic acid, ethylene, gibberellic acid, auxins, and cytokinins), proteins, and transcription factors (Verma et al., 2016; Gimenez et al., 2018). Understanding these mechanisms will not only help in saving important crops but also preventing economic losses. Searching suitable priming agents can significantly contribute to acclimation pathways of plants developed against the threats of stress-induced infections.

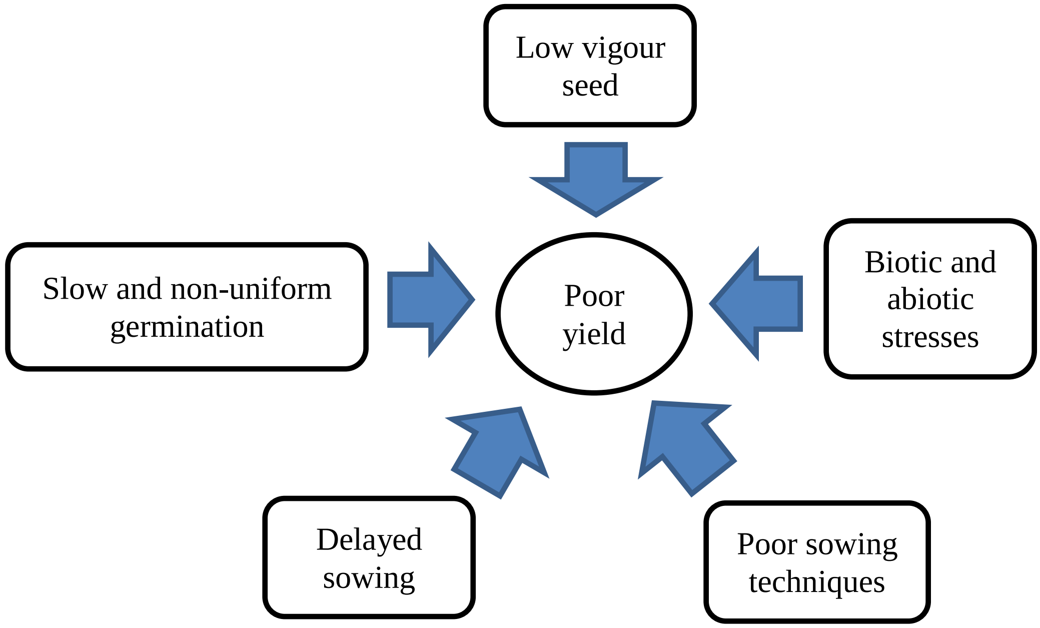

Figure 1: Basic issues in low productivity of crops

While attempting to maintain an optimum external environment for crops, the overdependence on natural resources and fossil fuel-based technology, over the years, has led to the gradual depletion of global water resources, escalating greenhouse gas emissions, and a gradual decline in productivity particularly in the high input-intensive agriculture systems. This scenario is likely to worsen and the brunt of the menace will supposedly be faced by rainfed agriculture systems globally on account of their inherent resource limitation. While 40 % of the world's and 68 % of Indian agriculture is rainfed, 42 % of the Indian food requirement is met through dryland agriculture (Singh et al., 2004). Climate change is a real intimidation to the developing world which unchecked, will become a major hindrance to poverty eradication. Besides, the contamination of the natural water bodies and soil strata through excessive agrochemical use coupled with improper irrigation techniques in intensive-irrigated agriculture systems call for alternative options under low-input sustainable agriculture systems with the ultimate aim of acquiring global food security.

2 POSSIBLE ALTERNATIVES

Throughout the history of agriculture, several methods have been adopted to achieve better crop tolerance to stresses and production in unfavorable environmental conditions. These entail breeding strategies (selection and hybridization, molecular breeding, genetic engineering) (Athar & Ashraf, 2009; Waqar et al., 2014), agronomic strategies (variety selection, date of sowing, soil management, irrigation) (Mariani & Ferrante, 2017; Lamaoui et al., 2018), physiological approaches (seed priming, foliar spray) (Bakhtavar et al., 2015), etc. The success of breeding techniques is often limited due to huge requirement of skilled manpower and energy, complexity associated with stress tolerance traits, tedious and costly methods, and ethical regulations. These drawbacks have forced the researchers to go for the alternatives which are simple and low-cost solution so that they are easily introduced at the field scale by resource-poor farmers.

Pre-sowing seed treatment (seed priming, seed coating, and seed pelleting), in this regard, is an effective strategy to overcome different stresses. This pragmatic and short-term approach is basically used as seed enhancement aimed at value adding or upgrading the quality of seed (Taylor et al., 1998). Such intervention involves the application of physical, chemical, and/or biological agents to stimulate seed germination, seedling vigour, and crop yield in a sustainable manner (Sharma et al., 2015). Seed priming is an effective pre-germination physiological method that mends seed performance and delivers quicker and synchronized seed germination (Matsushima & Sakagami, 2013; Nawaz et al., 2015) by prior exposure of seed to a stress situation, which endows plant to better withstand the future stress imposition (Yadav et al., 2011; Ibrahim, 2016). It involves soaking of seeds in water (hydropriming) or solutions of lower water potential (osmotic solutions) composed of polyethylene glycol (PEG) (osmopriming) or salts ($CaCl_2$, $CaSO_4$, KH_2PO_4, KCl, NaCl, etc.) (halopriming) prior to germination (Jisha et al., 2013; Paparella et al., 2015; Wojtyla et al., 2016). In priming, controlled imbibition is provided so as to induce the metabolic process of germination without actual germination and seminal root emergence (Binang et al., 2012; Nejad & Farahmand, 2012). Seed coating is a process of application of adhesive polymers with active ingredients (nutritional elements, plant growth regulators, insecticides, fungicides, and other chemicals) to the seed surface without altering its original shape or size (Avelar et al., 2012; Mandal et al., 2015; Pedrini et al., 2017). Seed pelleting came out as an advanced form of seed coating technology. The method includes enclosing of seed in a layer of inert material that may change the shape and size of raw seed, but produce a standard product (uniform round seeds) to facilitate improved planting (Mandal et al., 2015; Mei et al., 2017). Seed coating technologies are sophisticated and expensive (Sharma et al., 2015). Seed priming emerged as the most common method of pre-sowing treatments (Parera & Cantliffe, 1994; Jisha et al., 2013; Soleimanzadeh, 2013; Paparella et al., 2015; Lutts et al., 2016; Wojtyla et al., 2016).

3 ON-FARM PRIMING OPTIONS

In ‘‘on-farm’’ seed priming, seeds are soaked in water, surface dried, and sown in the field (Rashid et al., 2002). The term on-farm is used to differentiate it from the intensive agricultural systems using high input and advance technology for seed priming (Harris et al., 1999). This practice is very common in tropical environments or semi-arid agricultural lands as a low-cost and low-risk intervention. A plethora of priming techniques has been developed to enhance and stabilize field emergence, and those are categorized according to the priming agents used. The efficiency of these approaches is dependent upon certain factors like aeration and water potential of priming solution, light, temperature, priming duration, post-hydration drying, seed and storage condition, and plant species (Parera & Cantliffe, 1994; Wojtyla et al., 2016). Thus, it is essential to evaluate the efficacy of various priming options in different crops and agro-climatic conditions, and optimize our chosen priming technique.

3.1 Hydropriming

Slow and non-uniform germination of seeds induced the requirement of water-based seed priming. Hydropriming is a very simple, cost-effective, and eco-friendly technique which basically involves soaking seeds in water for a pre-determined time followed by re-drying to their initial moisture content (Farooq et al., 2006; Lutts et al., 2016). Submergence can also be performed in distilled water with or without aeration. Earlier, this practice was known as hardening, which was done by alternate soaking of seeds in water and drying before sowing. The process of seed germination occurs in three phases, viz., rapid water uptake or imbibition (phase I), lag or plateau phase (phase II), and protrusion of seminal root and resumption of growth (phase III) (Bewley, 1997). Hydropriming reduces the lag period, and ensures rapid and uniform germination for good stand establishment (Ahammad et al., 2014). Controlled seed hydration as a pre-sowing strategy triggers pre-germination metabolic activities in the form of cellular physiological, biochemical, and molecular changes (Figure 2) (Ibrahim, 2016; Wojtyla et al., 2016). Improved germination of hydroprimed seeds is a result of activation of enzymes (amylase, protease, phosphatase, lipase, etc.), ATP production, RNA and protein synthesis, DNA replication, detoxification of ROS and lowering of lipid peroxidation by antioxidant enzymes [superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and glutathione reductase (GPx)], accumulation of germination enhancing metabolites (proline, soluble sugars, etc.), higher utilization of seed reserves (proteins, carbohydrates, lipids, and phosphorus compounds), and other metabolic repairing mechanisms (McDonald, 2000; Ghassemi-Golezani & Hosseinzadeh-Mahootchi, 2013; Vaz Mondo et al., 2016).

Information on duration (maximum length of time) (Table 3) of hydration treatment can bring success at the farmer’s level. Mahmoodi et al. (2011) evaluated four hydropriming durations (6, 12, 18 and 24 h) to improve seedling vigour and field establishment of maize, and found 18 h to be the most effective priming period. In case of pinto bean, Ghassemi-Golezani et al. (2010) reported 7 and 14 h priming is sufficient to augment seed and seedling vigour, stand establishment, and grain yield instead of soaking the seeds for 21 h. For optimizing duration of hydropriming in mung bean, Shukla et al. (2018) chose five intervals of time viz., 2, 4, 6, 8, 24 h, and concluded 6 h of priming to be optimum as the germination responses were almost similar if the duration was increased after this priming treatment.

The major limitations associated with this technique include uncontrolled water uptake, which cannot be regulated because it is a property of seeds; and non-uniform hydration of seeds may result in unsynchronized germination (Taylor et al., 1998; McDonald, 2000; Di Girolamo & Barbanti, 2012). To overcome these challenges, drum priming is often used, where major focus is given on duration, temperature, and volume of water.

3.2 Osmopriming

Osmopriming is alternatively known as osmotic priming, osmotic conditioning or osmoconditioning. In this technique, seeds are soaked in osmotic solutions of organic compounds like PEG, mannitol, glycerol, sorbitol, etc. having low water potential so as to restrict the water uptake by seeds and allow the pre-germinative metabolic events to continue, but prevent the seminal root protrusion (Ashraf & Foolad, 2005). PEG with a molecular weight of 6000–8000 daltons having some osmotic potential (Ψs) is dissolved in water for seed treatment. Out of the different concentrations (5, 10, 15, and 20 %) of PEG solutions, Faijunnahar et al. (2017) reported 10 % is sufficient to improve the germination, seedling growth, and water relation behaviour of wheat genotypes. Sadeghi et al. (2011) tested the efficacy of PEG-6000 with different levels of osmotic potentials (-0.4, -0.8, -1.2, -1.6, and -2 MPa) and priming durations (6, 12, 24, and 48) on germination behaviour (percentage, mean time, index) and vigour of soybean seeds. Better results were observed in the seeds primed with -1.2 MPa for 12 h.

This technique is further classified as halopriming when the seeds are soaked in low water potential solutions composed of inorganic salts. Osmopriming/halopriming are also used for developing stress tolerances in plants (Table 2 and 3). Eivazi (2012) found wheat seeds primed with 2.5 % KCl for 16 h developed drought tolerance in plants besides increasing the grain yield. Rice seeds primed with NaCl @ 50 and 75 mM performed higher seedling vigor, osmotic stress tolerance potential, and overall crop growth than hydropriming (Jisha & Puthur, 2014). However, both of the priming treatments were able to modulate antioxidant enzyme activities, reduce lipid peroxidation of biomembranes, and increase the protein, carbohydrate, photosynthetic pigment, photochemistry, and mitochondrial activities of rice seedlings under salt stress conditions. A similar study of Goswami et al. (2013) revealed that rice seedlings conferred drought resistance by seed priming with 5 % of PEG-6000 and NaCl, which strengthened GPx activity and reduced peroxidative damage of the crop. Interestingly, priming effects of NaCl and PEG was not visible in chickpea under water deficit stress conditions (Kaur et al., 2002); priming with mannitol (4 %) and water gave better results in growth by modulating enzymes (amylase, invertase, sucrose synthase, and sucrose phosphate synthase) of sucrose metabolism (Kaur et al., 2002, 2005). Seed pretreatment with NaCl (50 mM) moderated the adverse effect of salt stress by modifying the antioxidant enzymes like SOD, CAT, and catechol peroxidase (CPX), enhancing accumulation of osmolytes (proline), lowering malondialdehyde (MDA) and H_2O_2 contents of plants, and improving growth and photosynthetic pigments (total chlorophyll, chlorophyll-a, chlorophyll-b, and carotenoids) (Saha et al., 2010). Application of PEG may cause disruption in aeration of solution due to its high viscosity (Paparella et al., 2015).

3.3 Solid Matrix Priming

In solid matrix priming (SMP) or matric conditioning, solid or semi-solid medium is used instead of liquid medium (Copeland & McDonald, 1995). This technique is accomplished by mixing seeds with a solid or semi-solid medium and specified amounts of water. By the virtue of the physical and chemical characteristics of the matrix, the water uptake by the seeds is restricted. In SMP, a small amount of liquid per unit of seed and solid particles is used. During SMP, water is slowly provided to the seeds and thus, slow or controlled imbibition occurs, allowing cell repair mechanisms to function (Jisha et al., 2013). Predominant solid matrices are exfoliated vermiculite, expanded calcined clay, bituminous coal, sodium polypropionate gel or synthetic calcium silicate (Kubik et al., 1988). Some locally available materials that are generally utilized as solid matrices are sawdust, charcoal and volcanic cinder and they offer the scope for reducing priming costs (Lorenzo, 1991). In the study of Lorenzo (1991) on SMP using sawdust, ground charcoal and volcanic cinder, soybean seeds responded favorably to shorter incubation periods, i.e., 1, 2, and 5 days. The longer incubation periods and higher water levels were harmful to the seeds because they encouraged fungal growth. SMP was also found to be effective in improving soybean germination by Mercado & Fernandez (2002).

3.4 Biopriming

Biopriming or biological seed treatment is the application of beneficial microbes in seed–plant–soil system to enhance plant productivity and simultaneously maintain the ecological balance. The process is accomplished by controlled seed hydration followed by coating of seeds with biological agents (Sarkar et al., 2017). The priming agents help in plant growth promotion by supplying nutrients to crops, enhancing resistance of plants to biotic and abiotic stresses, improving soil diversity (Singh, 2016), ameliorating soil structure, bioremeding the polluted soils (Mahmood et al., 2016). The technology basically aims at reduction of chemical inputs in our production system.

Farmers can treat the seeds with microbial formulations at the rate of 10 g kg^{-1} seed after soaking the seeds for 12 h and incubate at room temperature for 48 h to obtain microbial coating of seeds (Reddy, 2013). Carboxymethyl cellulose (CMC), gum arabic, rice water, etc. are used for adhesion of inoculums. The seeds are air-dried after incubation, and then used for sowing. Liquid formulations can also be used by the farmers as they mix well over the seed surface without any sticking agent. Root dipping of the seedlings for few hours before transplanting is also a common practice now-a-days. Biopriming agents are potential in promoting germination, controlling pathogens, and favouring growth and development in plants (Table 1). Microbial consortium of compatible microbes can also be used for better effects. Selection of microbes is an important step in biopriming as the growth-promoting abilities of microbes are highly specific to certain plant species, cultivars, and genotypes (Rakshit et al., 2015). Further, it can also promote synergistic interaction between microbes (e.g., *Trichoderma* and arbuscular mycorrhiza) (Meena et al., 2017). Arbuscular mycorrhizal fungi (AMF) (e.g., *Glomus* sp.) are getting special attention in biopriming techniques because of their multi-functional nature stimulating the growth and development of plants (Dhawal et al., 2016). Biopriming is a suitable tool to enhance the nutrient use efficiency in soil–plant–environment system (Meena et al., 2016).

Table 1: Some field experiments carried on biopriming

Crop	Biological agent	Method	Major effect	References
Boro rice	*Trichoderma* sp.	Seed inoculation @ 4 % of seed weight before 4 h of sowing	Higher grain yield	Rahman et al. (2015)
Maize	*Trichoderma harzianum*Rifai, (1969)	Seed inoculation @ 10 g kg^{-1} seed	Reduction of *Fusarium verticillioides* (Sacc.) Nirenberg (1976) and fumonisin infection, increased seed germination, vigour index, field emergence, yield, 1000 seed mass	Chandra Nayaka et al. (2010)
Barley	*Azospirillum* sp.	Seed inoculation @ 7 g kg^{-1} seed	Increased plant height, spike length, number of spike per area, grains per spike, 1000 grain mass, grain yield	Shirinzadeh et al. (2013)
Soybean	*Rhizobium* sp.	Seed inoculation @ 7.5 x 10^6 cells $seed^{-1}$	Increased germination, nodulation, seed yield, harvest index, nitrogen harvest index	Amule et al. (2017)
Pearl millet	*Pseudomonas fluorescens* (Flügge 1886) Migula, 1856	Seed inoculation	Enhanced germination, seedling vigour, plant height, leaf area, tillering capacity, 1000 seed weight, grain yield, induction of resistance against downy mildew	Niranjan Raj et al. (2004)

3.5 Nutrient priming

Nutrient priming has been proposed as a novel technique that combines the dual benefits of seed priming with an improved nutrient supply (Al-Mudaris & Jutzi, 1999). In nutrient priming, seeds are primed in solutions containing the limiting nutrients instead of being soaked just in water (Arif et al., 2005). Of the mineral nutrients, potassium plays an important role in imparting stress tolerance to plants (Cakmak, 2005). Seed priming in Zn^{2+} solutions improves grain yield of chickpea and wheat (Arif et al., 2007). Micronutrients are required in traces however, their deficiencies are quite common in crop plants (Abd El-Wahab, 2008). There are mainly 3 methods of micronutrient application in crops: application to soil, through foliar sprays and seed treatment (Johnson et al., 2005). Each method may affect plant growth distinctly. The use of micronutrient enriched seeds (seed priming) has been reported to be an easier and cost-effective strategy in overcoming micronutrient deficiencies (Harris et al., 1999; Rakshit et al., 2013). Seed priming has been shown to enhance the speed of germination (Deering & Young, 2006), reduce the emergence time, enhance seedling vigour (Harris, 1996) and obtain better stand establishment (Diniz et al., 2009), and increase yield (Yilmaz et al., 1998) in wheat, rice, maize, sorghum, chickpea, and soybean. There is evidence that sowing seeds enriched with micronutrients is also agronomically beneficial (Welch, 1986).

3.6 Redox priming

The cell processes are largely determined by "redox state". While redox state can categorically imply to the ratio of interconvertible oxidized and reduced species in a redox pair, lately this term is also correlated to define the cellular redox environment (Krebs, 1967; Schaefer & Buettner, 2001). It is opined that if the reduced redox state of a cell is possible to maintain, the extent of stress-induced damage can be significantly mitigated (Mittler, 2002). Srivastava et al. (2009) found that thiourea treatment to the seeds of Indian mustard (*Brassica juncea* (L.) Czem.) was helpful in maintaining the integrity and functioning of mitochondria in seeds as well as seedlings under salinity stress conditions. Srivastava et al. (2010b) treated *Brassica juncea* seeds with thiourea and observed different signaling and effector mechanisms to be regulated in a synchronized manner.

Seed priming with hydrogen peroxide was also reported in wheat (Wahid et al., 2007). Manjunatha et al. (2008) reported notable enhancement of seed germination and seedling vigour due to exogenous application of nitric oxide (NO) donors through seed treatment in pearl millet. Recently, Barba-Espín et al. (2012) reported that hydrogen peroxide could act as signaling molecule during the initiation of seed germination involving certain specific changes at proteomic, trancriptomic and hormonal levels. In the opinion of Draganić & Lekić (2012), priming with antioxidant substances like ascorbic acid, glutathione and tocopherol (vitamin E) was beneficial in increasing the vigour of sunflower seeds exposed to low temperatures. In sorghum, seed priming with cysteine reduced the injury caused by gamma radiations and the effects of cysteine were most prominent in primary root elongation (Reddy & Smith, 1978).

3.7 Hormonal priming

Plant growth regulators like auxins, cytokinins, and gibberellins can be utilised as a pre-sowing seed treatment to improve their germination and emergence in stress situations (Lee et al., 1998; Jisha et al., 2013). Particularly, abscisic acid (ABA) is extensively involved in plant responses to abiotic stresses such as drought, low temperature, and osmotic stress (Fujita et al., 2006). Besides inducing the expression of many salt-responsive genes (Chandler & Robertson, 1994), exogenous ABA application was found in some experiments to increase salt tolerance of the treated plants or plant tissues (Xiong & Zhu, 2002). At the molecular level, ABA is known to induce the expression of numerous plant genes (Rock, 2000). ABA priming showed increased rate of germination as compared to nonprimed seeds in Indian mustard (Srivastava et al. 2010a, b). The beneficial effects of gibberellic acid (GA_3) on germination are well known (Angrish et al., 2001; Radi et al., 2001). GA_3 (100 mg l^{-1}) applied as presowing treatment resulted in the highest K^+ and Ca^{2+} content in the shoots of faba beans (*Vicia faba* L.) and cotton (*Gossypium barbadense* L.) (Harb, 1992). Auxin has also been used for priming. In wheat seed germination, auxin treatments increased the hypocotyl length, fresh and dry mass of seedlings and hypocotyl dry mass (Akbari et al., 2007).

Improved replication in root tips has been found by hormonal and vitamin priming (Shakirova et al., 2003) which could be attributed to rapidly dividing root apical meristem, consequently leading to better growth. Moreover, hormone applications maintain the auxin and cytokinin ratios in the tissues, which inadvertently are responsible for enhancing cell division (Sakhabutdinova et al., 2003). Hormonal priming, specifically ethylene (ET) and chloroethylphosphonic acid (CEPA) has also been found to impart tolerance to cadmium toxicity (50 μM cadmium chloride ($CdCl_2$) to pigeon pea (*Cajanus cajan* (L.) Mill.) (Sneideris et al., 2015).

Some seed priming options adopted in various crops over time are presented in Table 2. Detailed description of seed priming agents and their respective concentrations along with the treatment durations are mentioned in Table 3. The major events of seed priming responsible for improved plant performances are shown in Figure 2.

Table 2: Seed priming methods developed for various agro-ecologies and their effect on imparting stress tolerance in agronomic crops

Crop	Agro-ecology	Treatment	Effect and protective mechanism	References
Cereals				
Rice	Rainfed	Halopriming (NaCl, KH_2PO_4), osmopriming (PEG), hydropriming	Drought and salinity tolerance by increasing carbohydrate, protein, and photosynthetic pigment content, modulating antioxidant enzyme activities (SOD, POD, GPx), reducing lipid peroxidation of biomembranes, enhancing photochemistry and mitochondrial activities of rice seedlings	Goswami et al. (2013); Jisha & Puthur (2014)
	Subtropics	Se and SA priming	Chilling resistance by increasing membrane stability, antioxidant activity, starch metabolism (α-amylase activity, total soluble sugar contents) of primed seedlings	Wang et al. (2016a,b)
Wheat	Arid and semi-arid	Halopriming ($CaCl_2$), hydropriming, chemical priming (H_2O_2), hormonal priming (auxin), choline priming	Salt tolerance by increasing antioxidant activity (SOD, CAT), leaf water relations, nutritional status (K^+, Ca^{2+}, NO_3^-, PO_4^{3-}), improving K^+:Na^+ ratio, reducing toxic elements (Na^+, Cl^-), RMP leakage of ions, enhancing root	Afzal et al. (2006); Wahid et al. (2007); Akbari et al. (2007); Salama et al. (2011)

			growth	
		Hormonal priming (ascorbic acid)	Drought resistance due to accumulation of proline and phenolics leading to membrane stability, tissue water maintenance, reduced oxidative damages	Farooq et al. (2013)
Barley	Arid	Nutrient priming (KH_2PO_4, $ZnSO_4$)	Drought and nutrient stress tolerance due to increase in root biomass influencing nutrient uptake, water use efficiency	Ajouri et al. (2004)
Maize	Sub-tropical semi-arid	Halopriming ($CaCl_2$)	Drought resistance due to well-developed root system facilitating higher water and nutrient supplies	Khan et al. (2015)
Triticale	Rainfed	Hydropriming, halopriming (KH_2PO_4)	Drought and salt tolerance is related with higher water uptake ability of seeds enhancing the relative water content of shoot, increased root and shoot growth	Yağmur and Kaydan (2008)
Pulses				
Mung bean	Subtropics	Halopriming (NaCl)	Salt stress tolerance by enhancing growth, photosynthetic pigments (chlorophyll, carotenoids), activities of antioxidant enzymes (SOD, CAT, CPX), accumulation of osmolytes (proline), lowering MDA and H_2O_2 contents of	Saha et al. (2010)

			plants	
Chickpea	Semi-arid	Osmopriming (mannitol), hydropriming	Drought tolerance by rapid hydrolysis of transitory starch	Kaur et al. (2002, 2005)
Soybean	Dryland	Nutrient priming ($ZnSO_4$), halopriming ($CaCl_2$), vitamin priming (betaine hydrochloride), hormonal priming (GA_3)	Soda saline-alkali stress tolerance by better osmotic adjustment, antioxidant defense system, membrane integrity, higher photosynthetic pigment contents, starch accumulation	Dai et al. (2017)
Alfalfa	Arid and semi-arid	Hydropriming, osmopriming (mannitol)	Salinity tolerance with higher activity of antioxidant enzymes (POD, CAT, SOD), accumulation of proline, stabilizing membranes by reducing MDA accumulation and electrolyte leakage	Amooaghaie (2011)
Sugar crops				
Sugarcane	Tropics and subtropics	Halopriming (NaCl), osmopriming (PEG)	Salt and drought tolerance by osmotic adjustment, antioxidant defense system	Patade et al. (2011)

Table 3: Seed priming agents and treatment durations applied for developing tolerances in some crops under drought and salinity stress

Crop species	Seed priming treatment	References
Rice	Halopriming (NaCl @ 50 and 75 mM) for 12 h; hydropriming with distilled water for 24 h; biopriming with *Trichoderma harzianum* @ 10 g kg^{-1} of seed for 24 h; spermidine (0.5 mM) priming for 24 h	Jisha and Puthur (2014); Yuan-Yuan et al. (2010); Rawat et al. (2012); Zheng et al. (2016)
Wheat	Hydropriming (16 h); halopriming (2.5 % KCl) for 16 h; osmopriming (10 % PEG) for 12 h; hormonal priming (2 mM ascorbic acid solution) for 10 h; choline priming (5 mM choline chloride) for 24 h	Patra et al. (2016); Eivazi (2012); Faijunnahar et al. (2017); Farooq et al. (2013); Salama et al. (2011)
Barley	Hydropriming for overnight (12 to 16 h)	Rashid et al. (2006)
Maize	Osmopriming with aerated solution of $CaCl_2$ (ψs -1.25 MPa) for 24 h	Khan et al. (2015)
Mung bean	Hydropriming (6 h); chemical priming with β-amino butyric acid solution (1.0 mM) for 6 h	Shukla et al. (2018); Jisha and Puthur (2016)
Pea	Halopriming with KCl and KOH @ 250 and 500 ppm (1 h)	Naz et al. (2014)
Soybean	Hydropriming (12 h) and hormonal priming (gibberlic acid @ 50 ppm) for 14 h; biopriming with *Trichoderma harzianum* @ 10 g kg^{-1} of seed	Langeroodi & Noora (2017); Khomari et al. (2018)
Indian mustard	Hydropriming with distilled water (18 h)	Srivastava et al. (2010a)
Sunflower	Hydropriming with distilled water (18 h)	Kaya et al. (2006); Moghanibashi et al. (2013)
Sugarcane	Halopriming (NaCl @ 100 mM) for 8 days	Patade et al. (2009)

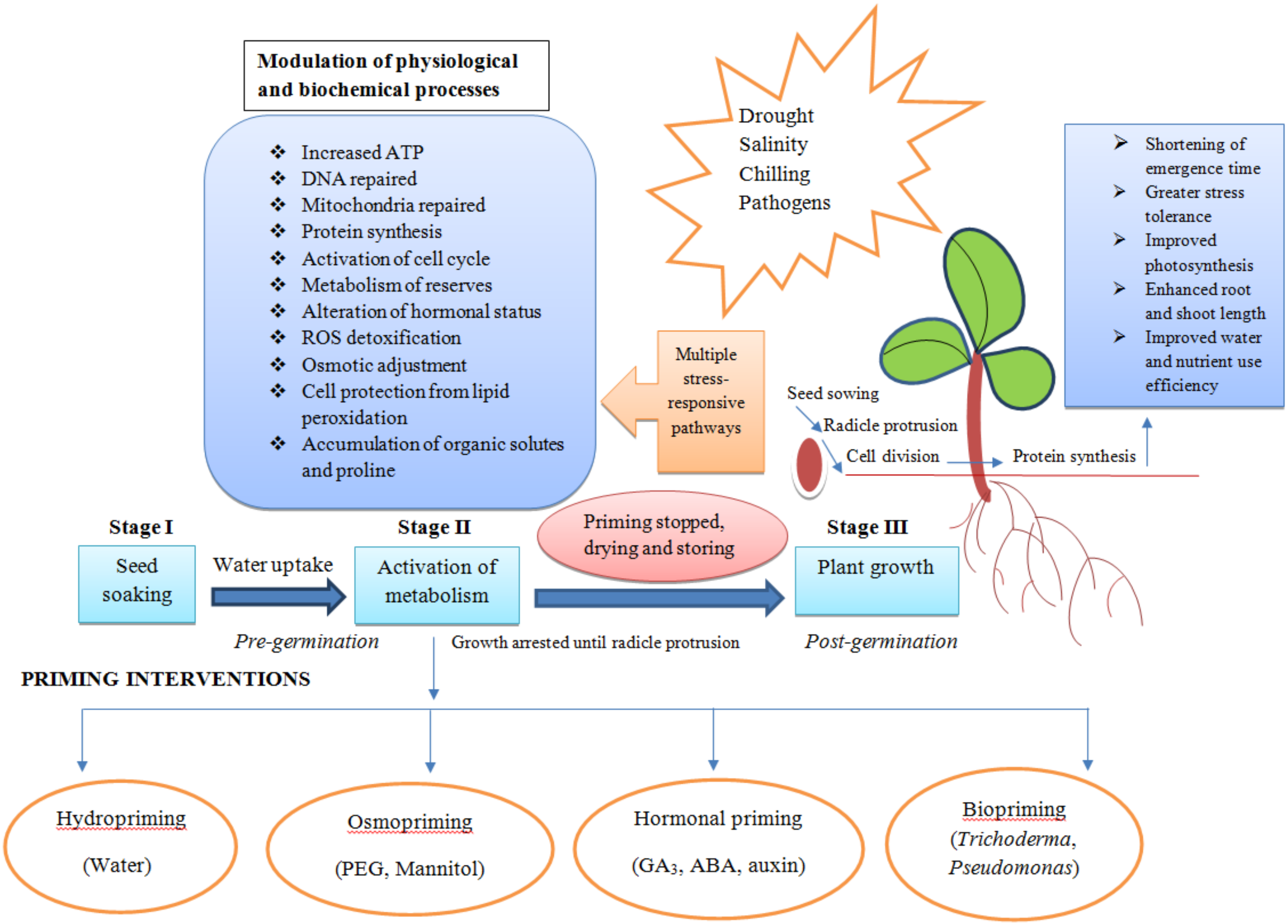

Figure 2: Schematic representation of the major processes induced by seed priming during pre- and post-germination stages

4 CHALLENGES IN ADOPTION OF SEED PRIMING

Many of the experiments which showed better results were practiced in greenhouse or controlled conditions, especially in the rainfed regions of Bangladesh, Pakistan, Nepal, Africa, and India. Their validation in field conditions is still unexplored. However, this customised method is gaining popularity, and emerged as a smart intervention across diversified agro-ecological regions. Harris et al. (1999, 2001) suggested on-farm seed priming can be revived through farmer-participatory approaches. Farm walks, group discussions, and other tools of extension should be adapted by the researchers/scientists. If the duration of priming is exceeded, then it may lead to seed or seedling damages. Special care is needed while transporting liquid inoculants and applying to the fields (Mahmood et al., 2016). Higher concentrations of priming agents may hamper or delay seed germination. The longevity of low vigour seeds are improved, but reduced in high vigour seeds (Varier et al., 2010). Reduced storability of primed seeds enhances the maintenance costs of farmers (Lutts et al., 2016). In hydropriming, the activation of the physiological processes are non-uniform because seeds are not equally hydrated (Girolamo & Barbanti, 2012). Heavy rainfall after sowing decays primed seeds in soils remaining saturated for a longer period of time (e.g., black soils) (Ramamurthy et al., 2005). Contamination of priming agents can heavily impair seed germination. The efficiency of the biological agents is often low or variable due to unfavourable environmental conditions (e.g., relative humidity, temperature, etc.), shorter shelf-life, low quality, and/or competition with local microbes (O’Callaghan, 2016). For better implementation of seed priming processes, crop species, location, duration of priming, priming agents, temperature, and storage conditions must be considered.

5 CONCLUSION

On-farm seed priming is an apt technology for the predominantly resource-poor farmers of the developing world. It is a simple, low-cost intervention which shows quick results in varied eco-systems ranging from arid and semi-arid tropics in India, Africa, the Middle East as well as in highly controlled temperate agriculture systems. Pre-sowing water hardening of seeds has been an age-old practice in several dryland agro-ecosystems. However, the recent advances in halopriming, chemical priming with KNO_3, KH_2PO_4, $ZnSO_4$, $MnSO_4$, etc., solid matrix priming, ascorbate priming, and redox priming have given this technique an added edge over the traditional system of seed hardening. Coupled with the success of modern science in agriculture, our understanding of the priming-induced responses of crops will open new vistas regarding their stress tolerance abilities, and devise further integrated and sustainable approach applicable in diverse agro-ecosystems. Biopriming with potent strains of *Trichoderma* spp. and *Pseudomonas* spp. among others is a stratagem of not only alleviating moisture stress but also imparting much needed biotic stress tolerance. Seed priming is known to activate certain signaling pathways during the early stages of plant phenology and result in quicker plant defence responses. Thereby, upon subsequent or future exposure to these biotic and abiotic stresses, a second signaling event would excite/stimulate the signaling proteins consequently amplifying the signal transduction, and therefore leading to more rapid and/or more intense activation of previously acquired defence responses (Conrath et al., 2006).

A better and refined transition from laboratory to field adaptability of the different seed priming methods is also needed, which essentially should be adjudged to extensive farmer participatory trials. While seed priming is indeed ascertained as a potential technology to mitigate the adverse effects of climate change and the ensuing alterations in water availability, extremes of temperatures, salinity stress, etc.; future work is needed on the usability of various priming options for varied agro-ecosystems and different crops.

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