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Seed priming - one small step for farmer, one giant leap for food security: II mechanism and manifestation

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Abstract

Seed germination, emergence and crop growth are often constrained by multiple environmental stress under field condition limiting productivity. Seed priming, a age old inexpensive technique, consisting of soaking seeds in priming agent prior to sowing, has been applied to different crops and conditions with varying degrees of success. To understand the significance of this potentially transformative agronomic strategy, we have reviewed here the detailed mechanism of seed priming at physiological and molecular level along with secondary metabolite production. Seed priming has significant positive impact on germination, crop health, yield, mitigation of biotic and abiotic stresses irrespective of its methods such as hydropriming, on-farm priming, halo-priming, osmopriming, osmo- hardening, hormonal priming, matrix priming, nutripriming or bio-priming. This technology could be effectively adopted as a strategy to increase food security in commercial agriculture.

Keywords: Germination, priming mechanism, secondary metabolite, imbibition

Introduction

Quick and uniform seed germination and seedling emergence are key factors of successful crop stand and robust growth in modern agriculture (Rajjou *et al*., 2012 [1]; Chen and Arora, 2013) [2]. Germination process begins with imbibition or water soaking by the dry seeds and ends with the elongation of radicle followed by protrusion of the root and shoot. All seeds stored under air dry conditions are subjected to various biochemical damage occurring at cellular level, resulting natural seed aging, lowering seed quality or even loss of viability, subsequently limiting seed germination and crop productivity.

Seed priming in an artificial initiation of pre-germination metabolic activities under controlled seed hydration with priming agents, but it interrupts actual radicle emergence (Ibrahim, 2016) [3]. Robust seedling health with exploitation of early vigour, efficiently mitigate multiple environmental stresses and enhance crop productivity. It also improves the germination of weak, damaged or aged seeds. The general mechanism of priming is to make the seed tolerant of desiccation and stimulatory to germination. In this paper, we will review recent developments in studies on seed priming with specific reference to mechanisms at physiological, biological and molecular level to understand its potential scope in commercial agriculture.

History

Since right from the start of agriculture, man accomplished that the majority seeds don't germinate simply and uniformly. Heydecker coined the word “Seed Priming” in 1973 and he successfully adopted seed priming to enhance seed germination and emergence underneath nerve-racking conditions (Heydecker *et al*., 1973) [4]. Theophrastus (372–287 BC) centered on seed physiology and steered that germination method is also briefly interrupted. He suggested the pre-soaking of cucumber seeds in milk or water to germinate earlier and smartly (Evenari, 1984) [5]. A like Greek farmers, Roman farmers also applied the science of seed priming in order to increase the germination rate with synchronized germination. Different types of seed priming technologies have been developed with the course of time. Among the seed priming techniques, the farmers of India, Nepal, Pakistan and Zimbabwe etc commonly adopt hydro priming. Centre for Arid Zone Studies (CAZS) prescribed “safe limits” for the on-farm seed priming of maize, upland rice, wheat, chickpea and sorghum. On farm seed priming could be a reliable and a wide applicable technology.

The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) has been promoting the use of chickpea in rice fallow cultivable areas of Bangladesh using on-farm seed priming. Seed priming with trace elements (i.e. Selenium, Nano Zinc) is given importance recently for not only better crop yield but also for its enhanced nutrition value.

Mechanism

Seed germination involves a series of steps ultimately leading to radical protrusion from imbibed seeds. Water content is very low in dry mature seeds (5–15%) which leads to stopped metabolic activities of seeds. The initiation of metabolic activities in such seeds leading to embryo development depends on suitable environmental conditions like temperature, water, and oxygen. Water uptake in germinating seed is basically a triphasic process, phase I, i.e., imbibition with a rapid initial water uptake, phase II as an activation phase with slight change in water content, and phase III with a further increase in water uptake that occurs as the embryo axis elongates resulting in resumption of growth (Rajjou *et al.*, 2012; Lutts *et al.*, 2016) [1, 6]. Before the end of activation phase, the germination process appears as a reversible process in which seeds can be dehydrated again in order to maintain viability during storage to facilitate reinitiation of germination under suitable conditions. The germination process of seed that has no problem with dormancy and coat permeability occurs in three phases when water enters inside dry seeds (Bewley *et al.*, 2013) [7]. The germination process may be divided into the subsequent 3 phases:

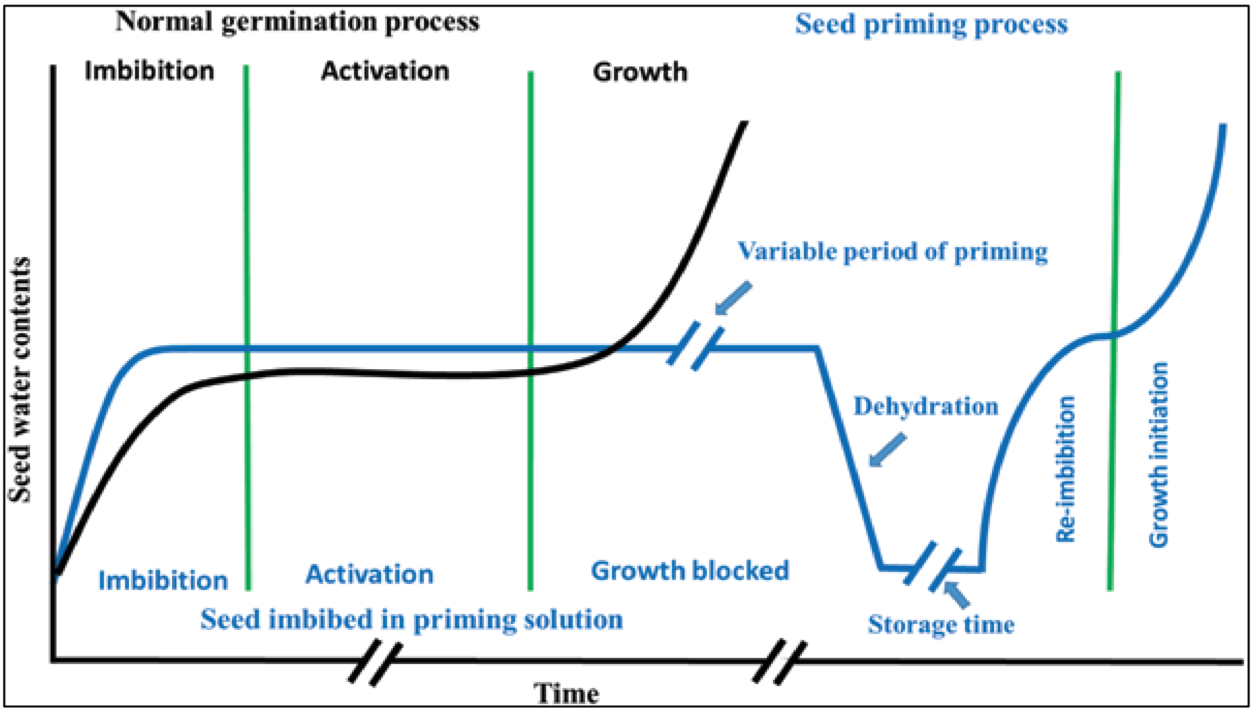

Fig 1: Schematic representation of the water uptake within the seed during standard germination and seed priming process. (Rajjou *et al.*, 2012) [1]

Phase I

The cell wall resistance towards cell expansion results in increase in turgor potential of the cell. Dry seeds when soaked in water lead to rapid uptake of water because solutes inside the seed cells decrease the turgor potential (phase I). Increased seed water potential during imbibition causes an increase in the seed water content. During seed imbibition, existing and new messenger ribonucleic acid (mRNA) leads to proteins synthesis in the embryo, DNA and mitochondria are repaired and synthesized (Rajjou *et al.*, 2012; Rosental and Nonogaki, 2014) [1, 8]. When the water potential of the cells of seed increases, the water uptake slows down and the seed enters lag phase (phase II).

Phase II

Phase II is known as the lag phase, in which the water potential of seed is counter balanced by the seed environment. During this phase, seeds absorb very small or negligible amounts of water extending over a relatively longer period, but significant metabolic activity is carried out associated with activation of enzymes and increased respiration. Therefore, by that time seeds can complete all its physiological pre-germination processes and get ready for radicle emergence. During this phase, the major metabolic changes related to germination such as new mitochondria and protein syntheses are initiated. Therefore, it is also called as activation phase (Di Girolamo and Barbanti 2012a, b) [9, 10]. Phases I and II are most sensitive stages of the germination process thereby essential for successful seed priming.

Phase III

When pre-germination embryonic processes are completed in phase II, the seed immediately moves towards phase III resulting in radicle protrusion through the seed coat and water and oxygen absorption rapidly increase (Welbaum *et al.*, 1998) [11]. This section will increase root growth, and its emergence coincides with biological process and enlargement (Rajjou *et al.*, 2012) [1].

Physiological impact

Physiological changes within a seed are one of the key parameters depicting seed priming effect more distinctly. As for example weakening of endosperm, reserve mobilization, and elongation of embryo cell was observed in the primed seeds with the GA treatment and higher number of mitochondria were also observed in osmoprimed leek cells

(Chen *et al*., 2001; Sung *et al*., 2008) [12, 13]. Structural and ultrastructural changes in seed during seed priming led to uniform seedling emergence and better seedling stand establishment (Galhaut *et al*., 2014) [14]. Seed priming with bioflavonoid enhanced both root and shoot elongation and increased the levels of photosynthetic pigments, flavonoids, and phenolic compounds (Singh *et al*., 2016) [15]. Throughout the embryogenesis, accumulation of ABA inhibits vivipary and modulates seed maturation. Aquaporins and Tonoplast Intrinsic Proteins, one of the major components mediated in primed seeds activates during imbibition process, which supplies water to the embryo and have impact on the speed of germination yet as stress resistance.

Biochemical impact

Primed seeds contain antioxidants such as POD, APX, SOD, and CAT which play an important role in enhancing stress tolerance. They guard the cellular membranes against the harmful effects of ROS such as H2O2, hydroxyl radicals, superoxide radicals and singlet oxygen (Bolkhina *et al*., 2003) [16]. Antioxidants like CAT, APX, and GR are activated during priming and activate antioxidant defense system (Paparella *et al*., 2015) [17]. SOD an antioxidative enzyme is an important scavenger of superoxide radicals, triggered during imbibition and reduces lipid peroxidation rate in plants (Yao *et al*., 2012; Rakshit and Singh, 2018) [18, 19], the increased activities of antioxidant enzymes permit the control accumulation of ROS during water uptake by seed (imbibition process) (Hsu *et al*., 2003) [20]. it had been steered that the buildup of ROS ought to be controlled tightly so as to play the role of positive regulator of germination, notably throughout osmopriming wherever less convenience of the water will cause a lot of production of ROS (Bailly *et al*., 2008) [21],

Molecular impact

Molecular level modulations are the key to any changes in the seed. The physiological and bio-chemical modulations are the result of molecular signalling. polymer repair mechanisms (NER, BER, HR, etc.) square measure currently considered pregerminated metabolism, vital for irruption of cell cycle activity (Wojtyla *et al*., 2016) [22]. Proper repair of damaged DNA allows the embryo cells to recommence cell cycle development and DNA replication; nevertheless, oxidative injury because of defective DNA repair mechanisms leads to cell death (Waterworth *et al*., 2011 [23]; Ventura *et al*., 2012) [24]. The major DNA repair processes such as nucleotide-(NER) and base excision repair (BER) are stimulated during the early seed imbibition phase (Cordoba-Canero *et al*., 2014) [25]. DNA replication; synthesis of RNA, DNA, and proteins; and accumulation of beta-tubulin are triggered with seed priming (Paparella *et al*., 2015) [17]. Prior to replication in ready seeds, repair of polymer harm happens primarily through polymer synthesis. In chickpea seeds, the role of polymer repair throughout seed priming was steered supported the expression analysis of genes concerned in polymer repair directly or indirectly (Sharma and Maheshwari, 2015; Wojtyla *et al*., 2016) [26, 22]. Upregulation of α- and β-tubulin subunits proteins are important for cell division mentioned by Varier *et al*., (2010) [27]. Aminoalkanoic acid regulates the cellular reaction potential, stabilizes the macromolecules and subcellular structures, and triggers the stress-responsive genes/proteins (Szabados and Savouré, 2010) [28]. Stress-responsive proteins (LEAs and HSPs), cell division and elongation, H+-ATPase activity, plasma membrane fluidity, and changes in proteome and transcriptome are the key elements to induce abiotic stress tolerance in plants (Gallardo *et al*., 2001; Zhuo *et al*., 2009) [29, 30]. 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 Kibinza *et al*., (2011) [31].

Impact on secondary metabolites

Priming has a clear impact on the production and storage of many antioxidants such as ascorbic acid, glutathione, α-tocopherol, etc. During priming partial digestion of starch occurs which significantly alters protein glycation and causes reaction between reducing sugar and amino group of several proteins (Ventura *et al*., 2012) [24]. It also alters the proline content in the seed (Kubala *et al*., 2015) [32]. Metabolites such as leucine, glutamate, fumarate, aspartate, threonate, or pinitol content of seeds of several species is hugely impacted by seed priming (Di Girolamo and Barbanti, 2012a) [9]. Methionine, an important precursor of polyamine and ethylene, is activated during the priming of seeds. Kinetics of ethylene production from its precursor ACC is altered by the priming technique (Wu *et al*., 2014) [33]. Even the small aliphatic molecule, polyamines influencing plant growth and development is greatly influenced by Seed priming.

Reserve mobilization

Secondary metabolites are the outcome of the certain metabolism and benefit the organism or system as a whole. This metabolites are actually the result of the rehydration process. This mechanism can be termed as Reverse Mobilization. During priming, respiration process is stimulated and rapid ATP synthesis occur to provide energy required for seed germination. To produce energy needed for seed germination. The improved adenosine triphosphate level when priming was detected in coniferous tree, cabbage, eggplant, oat, spinach, and tomato (Corbineau *et al*., 2000) [34]. Primed seeds require a high level of fuel as stored in endosperm to fulfil energy requirement for higher mobilization of reserve. This enriched energy level and metabolic rate of primed seeds and caused improved germination and stress-bearing potential.

Alteration in oxidative metabolism

During seed germination the stored food in embryo is utilized by the seeds for the radicle emergence. As the seeds respire oxidative reactions occur within the seeds. This oxidative reaction produces reactive oxygen species (ROS) which have a detrimental effect of seed protein and lipid. Accumulation of such ROS can cause structural aberration and hamper the emergence. There are certain anti-oxidants present in seed to neutralize the hazardous effect of ROS. The enhanced respiratory activities of mitochondria and increased activities of many enzymes such as NADPH oxidases, oxalate oxidases, peroxidases, and β-oxidation pathways were observed in the primed seeds. Among ROS molecules, H2O2 plays vital role as signalling molecule. The priming solution should be incorporated with strong ROS detoxifying system which promptly reduces the concentration of damaging molecules. This detoxification is distributed by associate economical system involving protein (i.e., SOD, glutathione enzyme, monodehydroascorbate enzyme, catalase) and protein inhibitor molecules (i.e., reduced glutathione, ascorbic acid). As a conclusion we can say that the production of ROS (i.e. H2O2, hydrogen sulfide, and nitric oxide) at lower concentrations are important as they acts as signalling molecules responsible for changing dormant to germination phase of seeds (Wojtyla *et al*., 2016) [22].

Pre-germinative metabolism

DNA and polymer each partially broken because of ROS reactions. However, DNA injury will be repaired by the precise restoration processes, whereas it's a lot of troublesome for polymer because of its severe sensitivity to injury caused by the ROS because of the shortage of injury recovery mechanism. Injury caused by ROS to proteins is each irreversible and reversible
(El-Maarouf-Bouteau *et al*., 2013) [35]. So priming acts as a healing procedure prior to germination for the reversible injuries occurred in DNA and RNA.

Alteration in transcriptomics

Transcriptomics is the procedure of examination of the transcriptome, the total set of transcripts of polymer shaped via order underneath specific conditions by means that of high-throughput approaches. Buitink *et al*., (2006) [36] have explicit that higher than 1300 genes is also controlled within the priming. Those genes whose expressions square measure controlled in priming procedure square measure usually classified supported the role of the parallel proteins (metabolism, regulation of cell cycle, process of DNA, regulation of transcription, stress reactions, cellular communications, and transport). But, an everyday portion of the recognized genes is however not explained.

Alteration in proteomics

Proteome depicts the whole set of the supermolecule gift at a selected time specifically biological sample and proteomic is that the comprehensive study that permits to spot and quantify these proteins. Quantitative protein analysis shows the alteration in supermolecule level among the various biological samples (Wong and James Cagney, 2010) [37]. Another different tool is gel-free firearm proteomic that is accustomed establish and quantify supermolecule at giant scale. Authors recorded the vital alteration in seventy-two completely different proteins iatrogenic by osmopriming. Most of those supermolecules vie their role in protein synthesis, chemical change and defence or unwellness hindrance and metabolism regulation.

There square measure 2 pathways for the alteration within the concentration of proteins within the seeds: first involves the synthesis of anew proteins, whereas the opposite needs digestion of accumulated proteins through proteolytic enzyme induction. Priming influence the activities of proteolytic enzymes and stimulate the expression of protease encryption cistron (de Lespinay, 2009) [38]. A collection of eighteen accumulating proteins because of osmopriming has been known in sugar beet seeds by Catusse *et al*., (2011) [39]. Hydropriming was additionally ascertained to activate drought tolerance in genus Medicago truncatula (Boudet *et al*., 2006) [40]. it's been confirmed by the proteomic analysis that drought tolerance character is related to the assembly of proteins from variant teams associated with late embryogenesis.

Alteration in metabolomics

Metabolome will be spoken because the entire set of the metabolites having smaller molecular mass occurring among a plant structure at a selected time. Thus, metabolome will be recognized as quantitative measuring of the whole set of compounds that square measure directly taking part within the metabolism of such sample. Plant metabolomics analysis has gained a special importance in genomics. Gibberellins square measure associate example that play a vital half within the smoothing of germination method however square measure reported to react with phenols or sugars, thus this property makes it a hindrance in isolation and/or identification of the many different metabolites (Wu *et al*., 2014) [33]. Complete understanding of any metabolome is hard, that the result of priming on any metabolome is additionally illusory and laborious to crack.

Impact of holistic "omic" seed priming methods

Biomarkers identification for sequenced primed seed is an important goal for plant physiologists. Every step of priming has its own configuration of activation/deactivation. There is no link between transcription and translation, inflicting in few circumstances a restricted correlation between template RNA and macromolecule levels. A bound protein made in incubation is also destroyed in dehydration, whereas the degree of degeneration is also tormented by the amount of drying. Macromolecule production may crop up as a consequence of the interpretation of prolonged template RNA erst made throughout seed development (Jisha *et al*., 2013; Boudet *et al*., 2006) [41, 40].

Manifestation

Primed seeds are healthier and able to mitigate multiple stress in the field condition. The major manifestation of seed priming was on germination (Table 1), growth and yield (Table 2) and stress management (Table 3).

Table 1: Effects of seed priming on germination

Method	Effect	References
Hydropriming	1. Improved germination and seedling vigour by hydropriming for 48 h and 36 h.	Farooq *et al*., (2006) [42]
	2. Emergence time shortened with seed priming at 3%-11% soil moisture contents when seed soaked were tap water at 30˚C for 12 h	Sakagami and Matsushima, (2013) [43]
On-farm priming	1. Prime with NaCl, KCl found heighest germination and overall growth of plant	Islam *et al*., (2012) [44]
Halo-priming	1. Improved germination and vigor index with KNO_3, KH_2PO_4, $MgCl_2$ and $MgSO_4$ priming solution.	Batool *et al*., (2015) [45]
Osmopriming	1.Highest germination percentage were found prime with $CaCl_2$, $ZnSO_4$ and KCl 2. Improve field crop establishment in 1% KNO_3 salt solution	Hasan *et al*., (2016) [46] Singh *et al*., (2012) [47]
Osmo-hardening	1. Osmo-hardeningr with Vitamin C increase germination , vigor index, shoot and root lengths	Mamun *et al*., (2018) [48]
	2. Priming seeds with KCl 20 mg L^{-1} for 24 hours to enhance germination and seedling vigor characters	Mohammed *et al*., (2020) [49]
Hormonal priming	1. Seeds primed with ascorbic acid as indicated by lesser time to start germination, MGT and T_{50} and higher GI, GE, FGP, FEP, radicle and plumule length and seedling fresh and dry weights	Basra *et al*., (2006) [50]
	2. Salicylic acid (SA) improved germination and reducing the time to start emergence, time to 50% emergence, mean emergence percentage, and improving the final emergence, emergence energy, emergence index	Rehman *et al*., (2011) [51]

Matrix priming	1. Solid matrix priming in combination with Trichoderma viride improve seedling emergence	Lingyun *et al.*, (2017) [52]
Nutripriming	1. B solutions improved the time to 50% germination, germination energy, final germination percentage, mean germination time, and germination index.	Farooq *et al.*, (2011) [53]
	2. Speed of germination and germination index was 1.4 times higher in seeds primed with $ZnSO_4$	Raj *et al.*, (2019) [54]
Bio-priming	1. Seed biopriming with Pseudomonas fluorescens improved the speed of germination, germination percentage, seedling length, dry matter production, vigour index.	Kokila and Bhaskaran, (2014) [55]

Table 2: Effects of seed priming on growth and yield

Method	Eggect	References
Hydropriming	1. Hydropriming for 48 h improved crop stand establishment, growth, yield and quality of crop.	Farooq *et al.*, (2006) [43]
	2. Highest vigor index, plant population m^{-2},maximum length of shoot and root were found seed primed for 30 hours as hydropriming.	Dey *et al.*, (2013) [56]
On-farm priming	1. Priming improved emergence and early growth and improve root at soil matric potentials.	Murungu *et al.*, (2003) [57]
	2. Seeds were primed (soaked in water overnight and then surface dried) increased grain yield, seedling emergence, plant height, number of pods/m^2, test weight.	Musa *et al.*, (1999) [58]
Halo-priming	1. Improve the germination, seedling growth, and seed yield using gibberellic acid (GA), polyethylene glycol (PEG), and NaCl.	Tian *et al.*, (2014) [59]
	2. Increased total yield by soaking of seeds in 3% KNO_3 solution for 30 and 40 hours at normal room temperature.	Maiti *et al.*, (2013) [60]
Osmopriming	1. Maximum fertile tillers, grains per spike, 1000-grain weight, grain yield and harvest index were observed in plants raised from seeds osmoprimed with $CaCl_2$.	Islam *et al.*, (2012) [61]
	2. Highest germination percentage, germination energy, germination speed vigour index was found when it was treated with KC1 and largest root when seeds were treated with NaCl.	Jafar *et al.*, (2011) [62]
Osmo-hardening	1. Primed seeds with $CaCl_2$, ascorbate and KCl proved better seedling growth and increase number of roots and fresh and dry mass.	Farooq *et al.*, (2010) [63]
	2. Seeds hardened with prosopis leaf extract @1% recorded higher seed yield, yield attributing characters and many seed quality characters.	Narayanan *et al.*, (2016) [64]
Hormonal priming	1. Highest tiller number per hill was recorded from 40% (v/w) in hormonal priming it was 150 ppm Salycilic acid.	Kareem *et al.*, (2013) [65]
	2. 50 Mm magnesium chloride improve crop yield.	Kareem *et al.*, (2019) [66]
Matrix priming	1. Solid matrix priming increase emergence and fruit yield (per plot 16.12 kg and per hectare 250.35 q).	Hu *et al.*, (2005) [67]
	2. Solid matrix priming (SMP) with T. harzianum increased seed germination vigor, germination index and seedling emergence, decreased mean emergence time, enhanced seedlings quality and photosynthetic characteristics.	Lingyun *et al.*, (2017) [52]
Nutripriming	1. Seed prime with different level of K (0,10,20 and 40 kg K_2O/ha) improve the grain yield.	Kalita *et al.*, (2002) [68]
	2. Seed priming with GA_3 (100 ppm) and ammonium molybdate increase plant height, number of leaves, total dry matter, test weight and grain yield.	Arun *et al.*, (2020) [69]
Bio-priming	1. Bio-agents (PSB and Psf-173) and microbial inoculants improved the plant growth, seed yield and quality of crop.	Sharma *et al.*, (2018) [70]

Table 3: Effects of seed priming on stress conditions

Method	Effect	References
Hydropriming	1. Improved emergence, stand establishment, allometry and grain yield during chilling stress.	Farooq *et al.*, (2008) [71]
Halo-priming	1. Priming with $CaCl_2$ (2Mm) increase the proline accumulation.	Anand *et al.*, (2012) [72]
	2. Increased total soluble sugars, proline, and glycine betaine. accumulation as well as decreased MDA and phenolic levels primed with $CaCl_2$.	Srivastava *et al.*, (2010) [73]
Hormonal priming	1. Reduced Na+ accumulation, increased content of K^+ and Ca^+, enhanced enzyme activities that involved in assimilation of secondary metabolism and decreased ROS and MDA contents with Salicylic acid (2 mM).	Sheteiwy *et al.*, (2018) [74]
	2. Enhanced CAT, POX, GR, and APX activities with Salicylic acid (0.2 mM)	Azooz., (2009) [75]
Bio-priming	1. Increased proline, total soluble sugar, K, and P, while reduced leakage of electrolytes and MDA content was found primed with Aqueous extracts of Padina pavonica/60 g L^{-1} or Jania rubens/80 g L^{-1}	Rinez *et al.*, (2018)[76]
	2. Seed primed with Leaf extracts of Typha angustifolia/40 g L^{-1} /48 h increased germination %, osmotic (proline, soluble sugars, K^+, P), chlorophyll, carotenoid, secondary metabolites (total phenolic, total flavonoid), while reduced electrolyte leakage and MDA	Ghezal *et al.*, (2016) [77]

Conclusion

Yield reductions due to environmental constraints, e.g. climatic aberrations, deteriorating resource base and increasing cost of agriculture inputs, requires inexpensive and sustainable intensification strategies to ensure food security. In this direction, seed priming may be one of the approaches to narrow down this yield gap by facilitating rapid and enhanced crop establishment that may also result in improved individual plant performance. The literature considered in our study encompassed the mechanisms involved in seed priming and its possible manifestation in germination, growth, stresses management and crop yield. Exploitation of early seed vigour through priming hardly require extra cost or labour but its crop specific en masse adoption at global scale may play a vital role in world food production mitigating multiple stresses at field level and enhancing agricultural productivity. Governmental institutions and policymakers may take appropriate steps to promote the adoption of seed priming for long term sustainability and food security.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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