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Seed Priming: Technique, Applications and Future Prospects in Vegetable Crops

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ABSTRACT: Horticulturists all over the world are struggling to meet the market's increasing demands for high-yielding quality vegetable crops. Seed priming presents a sustainable strategy to improve crop's physiological and field characteristics helping farmers and seed producers to ensure high crop productivity and minimise any additional input cost by ensuring optimum crop stand under normal as well as stress conditions. Current scientific trends suggest that priming may aid in the reversal of age and storage-induced seed deterioration. It aids in lowering the levels of reactive oxygen and reactive nitrogen species in seeds with better reserve mobilization, increased efficiency of antioxidant enzymes and DNA repair mechanisms. This review paper aims to summarise the latest trends in the seed priming works on the types, mechanism and efficacy of seed priming techniques in vegetable crops with a particular focus on its potential to recover aged seed *via* priming, along with highlighting the gaps in the current investigations that ought to be filled with future studies. The findings elucidate the great potential of priming as a technique to become a major part of integrative resource management and crop improvement programmes to address issues such as food security and crop productivity in the era of climate change.

Keywords: DNA repair, Germination, Priming, Seed quality, Stress resistance, Vegetable crops

INTRODUCTION

Vegetables are high-value, low-volume crops accounting a global seed market worth $7.17 billion in the year 2021 alone, projected to grow upto $11.36 billion at a CAGR of 6.78% in the forecast period by 2028 [1]. Vegetables are the fresh and palatable parts of herbaceous plants, including edible stems, leaves, and fruits, actively consumed for their high contents of antioxidants, vitamins and minerals [2]. This growth has been intensified by the current health trends of nutrient-rich diets and the impacts of COVID. Seed producers bear a greater responsibility for maintaining and ensuring seed quality and genetic purity from harvest to further sowing. Quality seed is not only the result but also the primary cause of successful vegetable production. The crucial importance of quality seed has been recognized since the ancient times of Manu stating, "Subeejam Sukshetre Jayate Sampadyathe," meaning "good seed in good soil yields abundantly."

In vegetable crops, fast and uniform field emergence is a vital pre-requisite for increasing crop stand and yield translating to eventual profits [3]. Two initial factors are important for successful raising of vegetable crops - germination and vigour of seedlings. It is extremely important to improve the germination and vigour of expensive hybrid seeds of vegetables for which priming can be the best option. It aids in successful crop development and productivity even under the increasingly narrowing ideal range of optimal productivity due to various biotic and abiotic stresses. Biotic stresses such as insect pests, diseases, and weed infestations and abiotic stresses such as droughts, extreme temperatures, water logging, high salt, phototoxic chemicals and mineral nutrient deficiency in soil are few major stresses predominantly limiting the crop productivity rates.

Seed priming is an easy and effective technique employed to improve the crop productivity under both normal and limiting conditions. Its use has been widely reported for synchronising seed germination, increased emergence and field establishment. Seed priming can help farmers minimize chemical usage to increase crop production through uniform seed germination especially under various biotic and abiotic stresses. The present review compiled and perused the available information on seed priming as a technique, its types, the underlying physiology and progress made in providing tolerance to seeds from various productivity limiting stresses with emphasis on vegetable crops. Emphasis was also given to the abilities of priming as a technique in repairing older naturally aged and accelerated aged seed lots.

SEED PRIMING TECHNIQUES

Seed priming is a presowing seed treatment, allowing controlled hydration of seeds to imbibe water and go through the first stage of germination but does not allow radicle protrusion through seed coat [4]. It is a low-cost pre-sowing technique that ensures rapid germination and uniform crop establishment [5], and may improve seedling emergence even under various abiotic and biotic stresses [6].

Germination is a complex tri-phasic process consisting of seed imbibtion phase followed by activation and growth initiation phase. Priming is an ameliorative technique introduced first in scientific circles by Heydecker in 1973. It is a form of controlled hydration of seeds, partially activating their metabolic processes, leading them to a physiologically active state but without initiating actual seed germination/radicle protrusion, and thereafter re-dried to their initial dry weight, thus suspending them into a lag phase [7].

Germination and seedling establishment are crucial phases in the plant life. Successful vegetable crop establishment is reliant on rapid and uniform seed germination, attaining their full viability and vigour potential even under adverse environmental conditions. Rapid and uniform germination in primed seeds is associated with a decrease in the time to water absorption, antioxidant enzymes activation, accumulation of germination-promoting substances, DNA repair during imbibition and improved osmotic adjustment [8-10].

Various seed priming techniques include hydropriming, osmopriming, halopriming, hormopriming, thermopriming, and solid matric priming to activate seeds, speed up the process of germination, improve seed germination and seedling vigour, and reduce the impact of environmental stresses [11].

Hydro priming: Hydro priming is the most well-known and cost-effective priming treatment where seeds are primed with water. It is an affordable, environmentally beneficial method that farmers can use as it involves no chemical substances. The main drawback of hydropriming is uncontrolled, rapid water uptake by seeds which may result in unequal degree of seed hydration and unsynchronized germination [12]. Despite its limitations, hydropriming technique has beneficial effects in pea [13], bitter gourd [14], faba beans [15], sugar beet [16], melons [17] and many other vegetable crops.

Osmopriming: Also known as osmo-conditioning, seeds are primed with osmotic solutions of polyethylene glycol (PEG), mannitol, glycerol, sorbitol and other osmolytes. The larger molecular size and low water potential of osmolytes slows down the absorption rate of water uptake, significantly decreasing the damage to the embryo [12]. Soaking of okra seeds in 15% PEG solution for 24 hours resulted in higher germination, canopy height, leaf area index, pod length and yield [18].

Halopriming: Halo priming is the process of seed soaking in inorganic solutions of sodium, potassium, calcium, nitrate and chloride salts etc. to accelerate germination. Halopriming of tomato seeds with NaCl (5%) and KNO_3 (5%) improved seedling vigour indices [11]. Brinjal seeds reported the highest germination when treated with 320 mM NaCl *via* regulation of ROS [19].

Hormo-priming: It is the process of treating seeds with hormones such as gibberellic acid (GA_3), ethrel, salicylic acid, jasmonic acid, kinetin, polyamines, and other growth regulators to promote germination and seedling growth. Seed priming using GA_3 has been shown to enhance germination in okra [20], onion [21], brinjal [22] and bell pepper [23]. Drum priming (a commercial form of hydropriming) with 24-epibrassinolide reported improved seedling growth along with reduced germination time allied with improved superoxide dismutase (SOD), catalase (CAT), and peroxidase (POX) activities in bell pepper seeds [24].

Nutri-priming: Nutripriming is the process of immersing seeds in solutions with essential macro and micronutrient salts, to increase the seed quality by boosting nutrient content. Micronutrients are necessary for the growth of plants because they are involved in two crucial processes in plants: photosynthesis and respiration.

Bio priming: Sukanya et al. [25] described bio-priming as an ecologically sound approach that includes inoculation of seeds using beneficial microorganisms, to preserve the physiological features of seeds to control infections. *Enterobacter* spp., *Trichoderma* spp., *Bacillus* spp. and *Pseudomonas* spp. are the most commonly utilised species for biopriming. Treatment of red cabbage seeds with dual consortium of rhizospheric-competent microbial agents - *Trichoderma harzianum* + *Pseudomonas fluorescens* followed by *Pseudomonas fluorescens* + *Bacillus subtilis* resulted in enhancement of growth and the micronutrient uptake of Fe, Mn and Zn in red cabbage [26]. Biopriming with rhizobacteria improved germination parameters of radish seeds under saline conditions [27].

Solid Matrix priming: Solid matrix priming is the act of incubating seeds inside a matrix (such as sand, clay, diatomaceous earth, peat moss, and vermiculite) with a limited amount of water [28]. The seeds are then separated from the matrix, cleaned, and dried again. Solid substances permit seeds to gradually hydrate while also stimulating the imbibition process. The use of solid matrix is instrumental in making seeds compete for available water, slowing hydration and lowering the risk of embryo damage [29]. Positive effects of solid matrix priming has been reported to enhance field performance in carrot seeds [30] as well as in onion seeds for improving germination and emergence under optimal and low temperature conditions [31].

Cell cycle inhibitors: Priming with cell cycle inhibitors like mimosine and hydroxyurea reported a decrease in germination parameters in fresh seeds but the treated seeds were able to maintain seed longevity for a longer time period than untreated seeds. Cell cycle inhibitors like mimosine were reported to suppress the seed deterioration by maintaining seeds in the G1-S phase. Results suggested that an improved seed survival rate after priming with cell cycle inhibitors is associated with better maintenance of DNA replication upon imbibition [32].

Nano priming: Nano priming is a novel form of seed priming that uses nanoparticles (NPs), including iron oxide, zinc oxide, silver nanoparticles, and titanium dioxide. Plants do not use the fertilisers/nutrients because they are washed away or degraded through exposure to sunlight as well as water. In recent years, nanoscale materials have been used for pre-treatment of seeds as well as for promoting seed germination, seedling parameters, and stress tolerance in crop plants. Nanoparticulate nutrient supply to plants allow for both the sufficient and controlled usage of nutrients at a particular site, necessary for plant growth enhancement. Gold (AuNPs) and silver nanoparticles (AgNPs) contributed to enhanced emergence and yield increase in nanoprimed onion seeds [33]. Acharya et al. [34] also reported AgNPs mediated germination, growth and yield improvement in watermelon seeds.

Magneto priming: It is dry seed pre-sowing treatment with magnetic field eliminating the mandatory requirement of hydrating the seed. Chiefly of two types- static (no change in flux density/ intensity over time) and pulsed/ time-varying (flux density or intensity changes at one or more frequencies), magneto-priming is being extensively experimented to speed up and synchronize germination and increase crop productivity in major vegetable crops [35]. Static magneto-primed with 50 mT for 2 hours hold the potential to alleviate the damages due to salinity stress by marked increase in germination, growth, yield, net photosynthetic rate, total chlorophyll and Na/K ratio in wheat [36]. Pulsed magneto-priming at 3% effectively increased seedling vigour upto 23% coincident with increase in activities of antioxidant enzymes and reduced ROS in cherry tomato seeds [37]. As reported by Bhardwaj et al. [38], activities of superoxide dismutase (SOD), glutathione reductase (GR) and catalase (CAT) were increased in magneto- primed cucumber seeds.

Radiation priming: Gamma radiation is a form of ionising radiation that can interact with and enter living tissues. Gamma rays have a substantial influence on nucleic acids, membranes, and proteins because they interact with them directly at multiple levels. UV radiation priming is also emerging as a novel priming technique, curated to increase the plant stand and yield while effectively lowering the impacts of biotic agents on vegetable crops. UV priming has been reported to improve germination rate, specific leaf area, root and shoot length and dry weight, two-fold higher flavonoid content, increased soya saponin and so imparting resistance in beans [39,40]; increased germination, biomass accumulation and photosynthesis and higher tolerance against salinity stress in lettuce [41].

X-rays have wavelengths ranging from 0.01 to 10 nm in electromagnetic radiation and with energy ranging from 120 eV to 120 KeV. Lenient X-rays with energies ranging between 0.12 and 12 keV are preferred in agriculture [42]. Little research has looked at how X-ray irradiation affects seed performance. Substantial improvements in morphological and ecophysiological properties have been documented in tomato seeds treated with X-rays [43]. However, there were alterations in leaf structure during seed treatment with high doses of X-ray radiation, which ultimately resulted in decreased photosynthetic efficiency.

PHYSIOLOGICAL AND BIOCHEMICAL MECHANISMS UNDERLYING SEED PRIMING

Germination is a complex tri-phasic process consisting of seed imbibtion phase followed by activation and growth initiation phase. Imbibition is known as the first phase (Phase I), which includes rapid adsorption of water by hydrophilic matrix of seed surface consisting of pectins and glycan polysaccharides causing cell wall hydrolysis, seed swelling and change in shape. Various metabolic processes during seed germination such as protein synthesis, resumption of respiratory processes, glycolytic and oxidative pentose phosphate pathway are initiated following the imbibition of water by seed alongside procession of DNA repair processes [44]. The second phase (phase II) is the lag phase, also known as the "activation phase", in which less absorption of water results in a slight increase in the weight of seed. The seed attains both metabolic and physiological activity and initiates mitochondrial maturation processes, protein synthesis, rapid reserve mobilization required for protrusion of radicle [45]. Priming entails progressing seeds to physiologically active state i.e., phase I and II without initiating actual seed germination/emergence (phase III) [46]. The lag phase in primed seeds is shortened because phase III preparation is not necessary. So after that, various benefits are added to seeds, such as uniform emergence of radicle, enhancement in growth rate, and increasing the number of seeds that will germinate. So, while priming, seeds that have already completed the first two phases of germination have the potential to accomplish the whole procedure rapidly when water is supplied during sowing. This considerably reduces the time taken for cellular operations to complete. As nucleic acid synthesis enzymes are activated, DNA content rises, resulting in higher content of total RNA and proteins [47]. It also repairs cell membrane damage caused by storage and drying.

Modification of seed ultrastructure

Generally, an alteration in the equilibrium between the embryo's development capacity and the mechanical resistance of the surrounding tissues is believed to be crucial in determining the potential of seeds to germinate [48]. In many horticultural crops, the endosperm membrane enclosing the embryo acts as a physical barrier, interrupting the germination process and preventing the protrusion of radicle. The hemicellulose xyloglucans are contained in the cell wall. An enzyme, xyloglucan endotrans hydrolase (XTH), cleaves xyloglucans and is associated with cell wall loosening. Another enzyme engaged in the breakdown of mannan-rich endosperm cell walls during germination and post-germinative growth of seedlings is endo-β-mannase. During priming, with the increased activity of XTH, production of endo-β-mannase is also enhanced, resulting in cytoskeleton remodelling, which is required for cell wall loosening. These changes hasten the germination process of primed seeds [29].

Change in seed water content

An apparent lag phase occurs after an initial intake of water during seed germination. The embryonic axis starts to grow following germination, resulting in an increase in the intake of water. Aquaporins regulate the passage of water through cell membranes, which is required for the commencement of metabolism. Aquaporins (AQPs) are transmembrane proteins that play an important role in plant water relations. Priming increases the AQPs boosting the transport of water all across the plasma membrane, which helps to deliver water to growing tissues and improves the germination ability of primed seeds [49]. This could provide a possible explanation for primed seeds absorbing water at a higher rate than non-primed seeds. The later part of the priming process includes drying of the seeds to its original moisture content leading to seed dehydration [50-52]. During cell dehydration, LEAs (late embryogenesis abundant proteins) concentrate to retain cellular structure and macromolecules through preventing protein aggregation and deactivation. This buildup of LEAs aids primed seeds in overcoming drought as well as other challenges like cold and salt stress [12].

Physiological and biochemical changes in primed seeds

Seeds undergo several physiological and biochemical changes during priming resulting in improved and uniform germination due to breaking of seed dormancy and better embryonic tissue expansion, reducing the lag time necessary for water uptake, hydrolyzing or metabolising inhibitors, triggering enzymes, and mobilising reserved food [28]. Priming increases the efficiency of processes in phases subsequent to seed imbibition. It leads to efficient mobilization of seed reserves, leaching of growth inhibitors, synthesis of proteins, repair of deteriorative DNA in seeds [48, 53] and activation of antioxidant enzymes which lower oxidative stress in seeds [54].

Management of oxidative stress

Seed priming encourages plants to effectively manage oxidative stress, implying that priming can help overcome abiotic stress responses in crops. Throughout the priming process, seed imbibition and consequent dehydration are accompanied by the generation of ROS (reactive oxygen species) [12]. When ROS interact with macromolecules, significant oxidative damage occurs. Due to the enhanced activity of antioxidant enzymes generated by priming, ROS generation during water intake can be controlled [48]. These antioxidant systems encompass superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), monodehydroascorbate reductase (DHAR), ascorbate peroxidase (APX), and gluthathione reductase (GSH), all of which contribute to scavenging of ROS [29, 55].

Reserve mobilisation

Imbibition marks the initiation of germination-related functions like respiration, energy metabolism, and reserve mobilization [12]. During seed germination, starch metabolism is essential as it regulates seedling vigour. Starch metabolism is triggered by the enzyme alpha amylase, which converts starch reserves into digestible sugars, which provide energy to the developing embryo [48]. Seed priming boosts the activity of enzymes like alpha amylase and dehydrogenase, which can hydrolyze starch macromolecules into smaller, simpler sugars while increasing ATP synthesis and respiration. Phytase, amylase, and protease all increase as a result of priming. Priming also improves the function of the enzymes malate synthase and isocitrate lyase, which metabolise lipids to sugars [28, 48]. Priming also regulates cell division and organelle organisation by ensuring that alpha and beta tubulin subunits are abundantly produced [44].

Cell cycle regulation

Essential cellular processes such as *de-novo* synthesis of proteins and nucleic acids, ATP production, deposition of sterols and phospholipids, activation of DNA repair and antioxidant activation are initiated as a result of rehydration. Repair of DNA is an important part of the pre-germinative metabolism, which is initiated as absorption of water begins and continues throughout imbibition and is associated with a rise in unregulated ROS levels [48]. To sustain genome integrity, each of the major DNA repair pathways (e.g., base excision repair and nucleotide excision repair) is initiated during the initial stages of seed water uptake [47]. Flow cytometric assessment from osmoprimed seeds of tomato demonstrated that priming induced positive results are related to an upsurge in 4C nuclear DNA in the S phase of cell cycle following imbibition of water displaying priming-induced improvement of DNA replication and further continuation of cell cycle at an higher level in primed seeds than untreated seeds [48, 56]. The cell cycle is suspended at the G2 phase during priming, permitting cells to synchronise germination upon sowing. Preactivation of cells plays an important role in the better performance of primed seeds. Priming may regulate the expression of cell cycle proteins such as cyclins, cyclin dependent protein kinases, and proliferating-cell nuclear antigens, hence regulating the cell cycle [44].

APPLICATIONS OF SEED PRIMING IN VEGETABLES CROPS

Priming and Seed germination

The benefits of seed priming in the production of high-yielding and high-quality vegetable crops are well documented (Table 1). Seed priming is a basic approach for enhancing early seedling emergence that kicks off multiple seed germination mechanisms. Seed priming has been shown in several studies to improve early seedling emergence and growth under stress situations as compared to untreated seeds [57]. Yadav et al. [58] reported higher survival rates in primed pepper seeds than unprimed seeds amidst cold and salt stress. Wu et al. [59] observed that solid-matrix priming increased the germination percentage of cauliflower and broccoli seeds than non-primed seeds under control and salinity stress conditions. Navitha et al. [60] recorded improvement in germination and other vegetative growth parameters in cucumber seeds after priming with KNO_3 (1%) and GA_3 (25 ppm). Adhikari et al. [14] studied the effect of several hydro-priming durations on the seeds of bitter gourd. When compared to unprimed seeds, hydro-primed seeds had the higher uptake of water and germination as well as seedling vigour indices. After hydropriming tomato seeds exhibited higher amount of soluble proteins and enhanced membrane integrity as compared to untreated seeds [61]. Anese et al. [62] reported that hydropriming of *Solanum lycocarpum* (Wolf apple) seeds for 15 days at 15°C is an effective strategy for improving germination of seeds and development of seedlings.

In tomato, enhanced emergence of seedlings and vigour, along with more leaf development, was reported when seeds were osmoprimed with PEG 6000 [63]. Priming of bittergourd seeds with PEG @ 5% for 12 hours improved germination, shoot and root length, fresh and dry weight, and seedling vigour index [64].

Priming of cucumber seeds with 50 mg L^{-1} salicyclic acid improved germination rate, uniformity, early growth, final

Table 1. List of research publications pertaining to seed priming in various vegetable crops

Crop	Method of priming	Major effects of priming	Reference
Tomato	Hydropriming for 15 days at 15°C	Higher germination, reduced mean germination time	[62]
	Priming with botanical extracts of wood apple, neem and white musale for 48 hours	Improved germination rates, seedling vigour indices, fresh and dry biomass	[139]
	Biopriming with 10^3 spores ml^{-1} of *Trichoderma asperellum* BHUT8	Higher germination and radicle length, high phenylpropanoid and polyphenol oxidase activities and lignification in primed seedlings	[140]
	Magneto-priming with 100mT for 10 minutes	Improved germination and growth parameters	[141]
Cabbage	Priming with urea for 8 hours	Higher germination rate	[80]
Guar	Biopriming with 10^6 spores ml^{-1} of *Trichoderma asperellum* BHUT8	Higher germination and radicle length and increased cellular defenses	[140]
Indian squash	Ascorbic acid @ 100 ppm and salicylic acid @ 50 ppm for 2 hours	Higher germination rate, germination index, plant height, vine length number of fruits per plant, fruit weight per plant and economic yield	[142]
Pepper	GA_3 @ 200ppm for 24 hours	Increased germination, plumule and radicle length, dry weight and vigour	[23]
	Marigold flower extract for 24 hours	Reduction in mean germination time, increased germination rate and index	[143]
	Drum priming with 24-epibrassinolide for 4 hours	Improved germination and seedling growth, higher enzymatic activities of catalase, superoxide dismutase and peroxidase	[24]
Chilli	KNO_3 @ 1%	Improved germination and field emergence	[144]
	Biopriming with 10^6 spores ml^{-1} of *Trichoderma asperellum* BHUT8	Higher germination and radicle length, increased cellular defenses	[145]
Cucumber	Magneto-priming @ 200 mT for 1 hour	Improved seedling emergence, germination and starch reserves and its mobilization. Higher water uptake	[38]
	Biopriming with phosphorus solublizing bacteria for 48 hours	Higher germination rate, Bartlett rate index- indicative of speed, mean root and shoot length, mean seedling dry weight and vigour indices	[145]
	KH_2PO_4 @ 0.001 M	Improved germination and seedling characters	[146]
	KH_2PO_4 @ 10^{-3} M and K_2HPO_4 @ 10^{-3} M	Improved germination characteristics	[125]
Onion	GA_3 @ 50ppm for 24 hours	Higher germination (%) and seedling vigour index- I, reduced mean germination time	[147]
	$ZnSO_4$ @ 0.5% for 10 hours	Improved speed of germination, germination (%), dry matter production and vigour index, enhanced the cell division and cell elongation at the meristematic tissue of radicle	[148]
	Hydro-electric hybrid priming (soaked in distilled water at 22°C for 5 hours followed by 10/ kv/cm electrostatic field for 40/ seconds and incubated at 96 hours in dark)	Enhanced activity of superoxide dismutase due to structural changes in the enzymes leading to efficient free radical scavenging, helped the self-healing of organelles and plasma membrane of embryo cells	[149]
Okra	Biopriming with 10^4 spores ml^{-1} of *Trichoderma asperellum* BHUT8	Higher germination and radicle length, high phenylpropanoid and polyphenol oxidase activities and lignification in primed seedlings	[140]
	Osmopriming with 5% PEG solution for 24 hours	Higher number of nodes per plant, width and length of fruit, height of plant at first and last picking, total yield and marketable yield per plant and weight of fruit	[150]
	Hydropriming for 12 hours and solid matrix priming with calcium aluminum silicate for 24 hours	Improved seed germination, seedling vigour and fruit yield	[151]
	Hydropriming, halopriming with $CaCl_2$ @ 1% with KNO_3 @ 1%	Synchronous germination and enhanced speed of germination in germplasm accessions IC411698 and IC89936	[152]
Wax gourd	KNO_3 @ 5% for 72 hours	Higher germination rate with lesser days to emergence and mean germination time	[153]
Pumpkin	Priming with 10% *Azospirillum* + 20% phosphobacteria + 20% *Pseudomonas fluorescens* for 12 hours	Higher plant growth and development as well as seed yield	[71]
Pea	H_2O_2 @ 20mM for 24 hours	Increased seed germination and seedling growth with lowered ABA levels	[154]

germination, index of emergence, length of plumule and radicle and number of roots as well as reduced time to start germination and 50% germination as compared to untreated seeds [65]. Singh and Pandey [66] reported an advancement in germination of onion seeds haloprimed with 150 ppm KNO_3. Raj et al. [67] observed that nutripriming with $ZnSO_4$ (0.025%) and borax caused enhancement in the seedling vigour index, Zn and B content in cowpea as compared to untreated seeds. Gandahi et al. [68] investigated the effects of nutripriming on cabbage and cauliflower after soaking them in various concentrations (0.01, 0.05, and 1%) of boron solution for 18 hours. The chlorophyll content of leaves and germination parameters were found to be higher at 0.01% boron concentration, however higher concentrations of boron were found to be inhibitory.

Microbial bio-inoculants offer ecofriendly approach towards improving crop productivity. Priming with microbial bio-inoculants (biopriming) can provide a resilient framework for reducing the input of detrimental agrochemicals and working directly on improving the soil health [69]. Biopriming involves a series of complex interactions between seed and plant microbiome in the rhizosphere in the form of exudation, organic matter decomposition, nutrient mobilization, remediation, competition, etc [70]. Frequently used fungal and bacterial inoculants include *Trichoderma*, *Rhizobium*, *Pseudomonas*, *Bacillus*, *Azotobacter*, *Azospirullum* sp., etc [69]. Sivakalai and Krishnaveni [71] observed that a combination treatment of *Pseudomonas fluorescens*, *Azospirillum* spp. and phosphobacteria improved fruit and seed yield and yield attributing characters of pumpkin cv. CO2. When compared to unprimed seeds, biopriming in chilli using *Trichoderma viride* at 60% (w/v) for 3 hours enhanced the germination rate, germination percentage, mean shoot and root length, seedling vigour index, and biomass production [72].

Kanwar and Mehta [73] observed that solid matrix priming of bitter gourd with perlite recorded the highest fruit yield in comparison to unprimed seeds. Almutairi and Alharbi [74] investigated the effects of silver nanoparticles (Ag NPs) on zucchini and watermelon seeds. Germination percentage, seedling growth, shoot length, chlorophyll content and antioxidants increased, but biomass and radicle length decreased in response to priming with silver nanoparticles (AgNPs). Dehkourdi et al. [75] found that anatase nanoparticles (TiO_2) increased reducing sugars, carbohydrates, proteins and chlorophyll content in primed pepper seeds.

Gupta et al. [37] subjected seeds of cherry tomatoes to various dosages of static and pulsed magnetic fields for 30 minutes and reported that germination parameters, peroxidase, and catalase activities were significantly increased. In the field performance of magneto primed seeds, an increase in production, quality, and number of fruits was also found. Hegazi and Hamideldin [76] observed that treatment in okra seeds with 400 Gy of gamma rays resulted in superior germination, seed quality, and yield, as well as increased photosynthetic ability. Low-dose gamma rays have been reported to boost the vitality of seeds, germination, and seedling growth in okra [77].

Priming and stress mitigation

Seed priming is among the best effective methods for improving seed tolerance to biotic and abiotic stresses. Priming agents and technique employed are central in reducing the negative impacts of both biotic and abiotic stressors on plant growth. Vermiculite primed broccoli and cauliflower seeds documented an increase in antioxidant activity of enzymes like peroxidase and catalase, proline, sugars and proteins in the seedlings, thus imparting salinity tolerance to the crop [59]. Pereira et al. [78] found that osmo-priming in carrot seed boosted seedling emergence under high temperature and water stress conditions.

Abiotic stress mitigation

Plants are subjected to abiotic stresses throughout their lives in natural habitats, which have a negative impact on their growth and production. Abiotic stresses result from unfavourable environmental conditions for plant development and reproduction, whereas biotic stresses are caused by specific damaging living organisms such as bacteria, fungi and insects [79]. Drought, heat, cold and salinity are just a few of the factors that are endangering crop output. Plants regulate several physio-biochemical mechanisms to counteract the impacts of such abiotic stresses. Seed priming, a practicable strategy has been used effectively to produce proper stand establishment under normal and stressed situations (Table 2). Seed priming of Chinese cabbage (*Brassica rapa* L.) using KNO_3, urea and distilled water at 20°C for 8 hours exhibited enhancement in germination and seedling vigour under drought stress when compared to non-primed seeds [80]. Cauliflower and broccoli seeds subjected to solid-matrix priming with vermiculite and H_2O exhibited enhanced germination and other growth

Table 2. List of research publications pertaining to seed priming induced abiotic stress tolerance in various vegetable crops

Crop	Method of priming	Stress	Major effects of priming	Reference
Tomato	Osmopriming with pyroligneous acid @ 2:100 for 24 hours	Aluminium toxicity (0.5mM)	Improved seed germination, seedling growth and antioxidant defenses (glutathione reductase, peroxidase, superoxide dismutase, catalase, ascorbate peroxidase) lowering H_2O_2 and MDA levels, increased proline and soluble proteins accumulation	[105]
	Biopriming with residual fractions of *Ulva lactuca* extracts	Salinity	Higher concentrations of glycine betaine produced aiding in osmotic adjustment, ROS scavenging and subcellular structural stabilizations	[104]
	KNO_3 @ 0.75% for 24 hours	Suboptimal growing conditions	Increased field emergence, mean emergence time due to higher total sugars and phenolics	[155]
Radish	Rhizobacteria strains; *Agrobacterium rubi* strain A16, *Burkholderia gladii* strain BA7, *Pseudomonas putida* strain BA 8	Salinity	Improved seed germination under saline conditions	[27]
Lettuce	UV-C @ 0.85 kJ/m^2 for 1-4 minutes	Salinity	Improved germination characteristics and higher total phenolics, flavonoids, DPPH scavenging activity and total antioxidant capacity	[41]
Cucumber	Melatonin @ 500 µmol/L	Salinity	Increased lateral root formation, promoted total antioxidant and peroxidase levels, upregulation of genes associated with cell wall formation, carbohydrate metabolism, catalytic activities, catabolism of ABA and gibberellic acid biosynthesis	[156]
	$CaCl_2$ @ 2 mM	Salinity	Increased proline content under salt stress	[157]
	Triacontanol @ 50 µM for 12 hours	Salinity	Increased seedling emergence rate, uniformity and early growth, shoot and root length, dry weight of seedlings	[83]
	KNO_3 @ 5%, K_2HPO_4 @ 1% for 24 hours	Low temperature	Higher germination rate was obtained from 5% KNO_3 and highest seedling fresh weight from 1% K_2HPO_4	[158]
Bottle gourd	KNO_3 @ 4% at 20ºC for 6 days	Low temperature	Enhanced germination capacity and emergence rates at 15°C	[159]
Muskmelon	Halopriming with NaCl @ 150 mM for 36 hours at 20°C	Salinity	Increased shoot dry weight in primed seeds with increased antioxidants enzyme activity, soluble carbohydrates and proline content with reduced MDA levels and seed membrane damage	[160]
Watermelon	2.5% KNO_3 solution for 6 days in dark containing 1 and 3µM of methyl Jasmonate (MeJA)	Low temperature (15°C)	Improved germination and emergence characteristics	[161]
Bell pepper	KCl @ 10 mM for 36hours	Salinity	Incresed chlorophyll and proline content under salt stress	[162]
	Thiourea @ 1.3mM for 24 h at 25°C	Cold stress (4°C)	Increased expression of PROX1, CaWRKY30, osmotin, SOD, CAH, and Cu/Zn genes under cold stress	[163]
	10 mM Glycine betaine	Salinity	Decreased MDA levels and enhanced superoxide dismutase activity and proline content	[164]
Brinjal	3% KNO_3 solution with 0.1mM salicylic acid for 6 days	Low temperature (15°C)	Improved final germination percentage, germination rate and germination synchrony	[124]
Cauliflower	Solid matrix priming Seed: Vermiculite:H_2O::1:1.5:1 for 2 days in dark	Salinity	Increase in antioxidant enzymatic activities, soluble protein, soluble sugars and proline	[59]
Broccoli	50 mM KCl for 10 hours at 28 °C	Salinity	Increased water relation traits (i.e., osmotic and water potential and hydraulic root conductivity) and glucosinolate	[165]
	Ascophyllum nodosum seaweed extract	Water stress	Reduced stomatal closure with increased total phenolic, flavonoid and isothiocyanate content	[166]
Pak choi	Priming with 10µM sodium nitroprusside (NO donor)	Salinity	increased salt tolerance by boosting biochemical and physiological pathways	[167]
Okra	Alpha-tocopherol @ 200 and 300 mgL^{-1} for 16 hours	Salinity (100mM NaCl)	Improved fresh biomass, yield, sugars, total soluble proteins, glycine betaine content and activities/ concentration of antioxidants (ascorbic acid, total phenolics, GPX, SOD and protease)	[168]

Contd.

Crop	Method of priming	Stress	Major effects of priming	Reference
	Biopriming with 10^{-7} CFU of *Pseudomonas fluorescens*	Drought	Increased relative water content (RWC), metabolite accumulation such as sugar, free amino acids and enhanced activity of non enzymatic antioxidants; phenolics, ascorbate (AsA) and glutathione (GSH) and reactive oxygen species scavenging enzyme like superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) and guaiacol peroxidase (GPX) under drought stress	[169]
Pea	Aqueous extract of *Typha angustifolia* @ 40 g/L	Salinity	Enhanced maintenance of membrane integrity, proline content, total soluble sugars, chlorophyll and carotenoid content	[170]

parameters in seedlings under salt stress [59]. Napa cabbage seeds (*Brassica rapa* subsp. *perkinensis*) reported good germination and seedling growth in salt-stressed conditions following hydropriming with distilled water in dark at 20°C for 10 hours [81]. Khan *et al.* [82] reported that uniform emergence of seedlings was observed under salinity conditions when pepper seeds were primed with acetyl salicylic acid and salicylic acid. Cucumber seeds primed with 25 and 50 µM triacontanol performed better than unprimed seeds under saline conditions [83]. Khan et al. [82] reported that hot pepper seeds primed with 1 mM solution of NaCl showed improved vigour of seedlings and good plant stand under salt stressed conditions. Ghassemi-Golezani and Esmaeilpour [84] proposed that with the use of KNO_3 (3%) as priming treatment, the emergence and establishment of cucumber seedlings was speeded up especially when cucumber sown under low temperatures. Germination indices in radish seeds were enhanced under salt condition after bio-priming utilizing rhizobacteria [27]. Matric-priming enhanced field emergence of carrot and onion seeds under low temperature conditions [30]. Lettuce seeds when primed with 0.85 kJm^{-2} UV-C rays resulted in mitigation of severe salt stress possibly due to improved growth parameters, antioxidants, phenolics, increased free radical scavenging activity and higher K^+ and Na^+ ion uptake and thus, increased Na^+ ion concentration in leaf tissues [41].

Biotic stress tolerance

Treatment of vegetable seeds with priming agents like salicylic acid, jasmonic acid and ²-aminobutyric acid (BABA), etc hold a great potential to enhance plant resistance, reducing the crop damage by generating long lasting defence responses against pests and pathogens at physiological and molecular level (Table 3). Worrall et al. [85] reported enhanced defence gene expression in tomato plants hindered pests like red spider mite, tobacco hornworm caterpillar, green peach aphid following the use of jasmonic acid and β-aminobutyric acid (BABA) and also provided protection from *Botrytis cinerea* and powdery mildew. Early blight disease of tomato was attenuated by biopriming with arbuscular mycorrhizal fungus [86]. Priming of brinjal seeds with salicylic acid @ 0.5 mM for 3 hours led to reduced *Verticillium* wilt incidence with an increase in germination and seedling vigour. The induced resistance following salicylic acid priming could be chalked up to an increase of 1.7, 2.9, 2.1, 2.5 and 2-fold increase in gene expression of auxin (IAA27), mitogen activated protein kinase (MAPK1), glutathione peroxidase, chitinase and β-1,3-glucanase, respectively [87]. Bio-priming with *Trichoderma* sp. has also been shown to inhibit damping off disease of soybean [88], cucumber [89] and pea [90]. Cabbage seeds treated with a low dosage of UV-C have been reported to be resistant to black rot possibly due to higher expression of PR-protein (β-1,3-glucanase and chitinase) related defense enzymes [91]. Priming of cucumber seeds with *Pseudomonas syringae* pv. *lachrymans* and *Xanthomonas axonopodis* pv. *vesicatoria* reported higher fruit productivity and improved resistance against insect pest *Spodoptera litura* under *in vitro* and field conditions [92]. Transcriptional studies of the primed seeds demonstrated upregulated ethylene, salicylic acid and jasmonic acid signalling.

Biopriming of tomato seeds with *Trichoderma asperellum* (1 x 10^7 CFU mL^{-1}) and *Ochrobactrum* sp. (1 x 10^8 CFU mL^{-1}) improved seed germination while reducing the incidence of fusarium wilt which could also be attributed to priming induced increased accumulation of total phenol and antioxidant enzyme activities [93]. Many fungal endophyte strains are increasingly employed to deter aphid and leaf miner infestation and curb damages associated with yield losses in French beans [94]. Raj et al. [95] reported increased vegetable yield in okra seeds for two years on priming with both *Trichoderma viride* and *Pseudomonas fluorescens*.

Table 3. List of research publications pertaining to seed priming induced biotic stress tolerance in various vegetable crops

Crop	Treatment	Major effects of priming	Reference
Tomato	Biopriming with *Trichoderma asperellum* BHU P-1, *Ochrobactrum* sp. BHU PB-1	Resistance against fusarium wilt through increased total phenol content and augmenting the activity of peroxidase (PO), phenylammonia lyase (PAL), polyphenol oxidase (PPO) and chitinase as well as activating phenylpropanoid pathway (lignin deposition).	[93]
	Sodium chloride	Increased tolerance to *Ralstonia solanacearum*, the causative agent of bacterial wilt of tomato	[171]
	Pseudomonas putida isolates (M80, M96 and T109)	Resistance against Fusarium wilt, *via* phenylpropanoid pathway and pathogenesis-related protein activation	[172]
	Plant-derived priming agents-eugenol and anise oil	Enhanced resistance against heat stress and tomato yellow leaf curl Thailand virus (TYLCTHV) infection.	[173]
	Priming with silicon	Increased transcript levels of defense signature genes and activities of antioxidant enzymes against early blight resistance	[174]
Cucumber	Chitosan @ 2.5mg/mL	Providing resistance aginst powdery mildew	[175]
	Bacillus amyloliquefaciens MIC6 and *Pseudomonas aeruginosa* MTCC2581	Manages Fusarium wilt both in greenhouse as well as in field conditions	[176]
	combination of *Trichoderma harzianum* and *Trichoderma virens*	Reduced damping off caused by *Pythium aphanidermatum*	[89]
Brinjal	Salicylic acid	SA reduced *Verticilium* wilt incidence to 39.25% along with higher PR proteins (β-1,3-glucanase and chitinase) related defence enzyme and increased gene expression of IAA27, MPK1,GPX, chitinase and β-1,3-glucanase.	[87]
	Salicylic acid	SA reduced *Verticillium dahliae* by forming papillae, hypersensitive reaction, cell wall thickening	[177]
Chilli	*Bacillus* sp. BSp.3/aM	Anthracnose disease incidence reduced up to 20% with increased activity of phenylalanine ammonia-lyase (PAL), peroxidase (POX) and lipoxygenase (LOX)	[178]
Okra	Plant growth promoting fungus (PGPF) *Penicillium* sp. EU0013	Used against *Fusarium solani* which is causal agent of root rot of okra and found reduced disease severity and seedling mortality	[179]

Priming induced recovery of aged seeds

Seed deterioration is an inexorable part of seed storage life, leading to loss of seed quality, viability and vigour due to the adverse effect of combinational environmental factors. Priming treatments can play an important role in alleviating and minimizing ageing-associated damage. There is an obvious time gap between the time of seed harvesting and next sowing. Seeds are stored in order to sustain their good physical and physiological condition from the time of harvest till planting [96]. Natural ageing refers to the seed stored at ambient or cold storage houses till the next seed sowing arrives. Accelerated aged seed is an another kind of aged seed experimentally obtained by researchers to predict the storage induced changes in the seeds over a period of months in a couple of days. It is a benchmark concept of rapid seed ageing by subjecting them to higher temperature and relative humidity within a short period of time in order to investigate relative seed storability.

Both natural and accelerated ageing leads to reduction in germination and seedling vigour indices. Ageing also leads to membrane deterioration and also influences enzymatic activities *viz*. peroxidase, catalase, ±- amylase. Total soluble sugars, total free amino acids and free radicals accumulate to higher levels in aged seeds while ascorbic acid and ±-tocopherol reduced with ageing. Ageing also increases the degradation of DNA, production of ROS like superoxide to higher levels, inhibits catalase activity and also increases protein and nucleic acid degradation [97].

Oxidative stress in aged seeds is the prime cause of decline in seed quality and is associated with the higher reactive oxygen species (ROS) and reactive nitrogen species (RNS) accumulation and weakening of seed antioxidant machinery [98,99]. Lack of control over oxidative processes is one defining character of short-lived seeds like onion. Aged seeds report significant loss in the total phospholipids early during storage as reported in onion and cucumber seeds [100]. Lipoxygenase enzyme plays a pivotal role in the depletion of non-polar lipids and fatty acid reserves or even membrane lipids.

Deterioration of seed quality correlates with the loss of seed viability and vigour under field conditions. A negative relationship has been widely reported between germination and aged seeds [101]. Speed of germination is the first component of seed vigour that decreases in association with seed ageing. A drastic decline in the speed of germination can be observed in seeds vis-à-vis longer time taken for the commencement of germination in aged seeds than control seeds. Ageing also significantly alters the biochemical composition of seeds [102] with gradual decline in the seed reserves. Priming has been reputed to improve the seed quality by alleviating ageing induced damage by decreasing lipid peroxidation and increased activities of anti-oxidative enzymes like catalase, peroxidase, superoxide dismutase, acid phosphatase, glutathione reductase, etc [103-105]. Priming increased the activity of malate dehydrogenase, involved in the conversion of lipids to utilizable form of sugars during germination as reported in KNO_3 primed okra seeds [106], reduced the damage to the embryo cell ultrastructure caused by lipid peroxidation and enhancing seed vigour and storability [107].

Patil et al. [108] reported the highest specific activity of amylase in 0.5% calcium primed seeds and highest acid phophatase activity in 0.5% magnesium primed onion seeds. Amylase activity is observed in endosperm until the starch reserves are exhausted in endosperm after which it falls to zero. Amylase activity was promoted by gibberellic acid and inhibited by benzyl adenine and abscisic acid as reported during germination and early seedling growth in *Polygonum pensylvanicum* seeds [109].

Protein stability in seeds gets reduced with ageing and prolonged storage. Rapid ageing increased phosphatidic acid levels and lipoxygenase activity in onion and cucumber seeds [100]. Sharma et al. [110] reported 100% germination in mung bean seeds after hydropriming of 8-day controlled deterioration. Hydroprimed seeds reported reduced electrical leachates and higher levels of proteins, catalase, amylase and SOD, higher RNA levels than non-primed or controlled seeds. DNA integrity of chloroplast and mitochondrial organelles were also reported to be significantly higher in primed mung bean seeds than non-primed seeds, indicating priming induced early activation and repair of the pre-existing mitochondria and thus, greater transcript peaks of chloroplast and mitochondrial genes upon imbibition [111].

The widely reported ability of reversing the age-related seed deterioration of primed seeds could be attributed to leaching of growth inhibitors, protein synthesis, increased levels of antioxidants lowering the ROS levels and repair of damaged seed DNA [53, 54]. In brinjal (*Solanum melongena*) seeds, seed priming with 100 ppm GA_3 was found to be the most effective for enhancing germination and vigour indices in both high (naturally aged seeds) and low vigour seeds (accelerated aged seeds) 12 months after storage [112]. Osmopriming with -0.5 MPa salt solutions of KNO_3 and NaCl were reported to be effective in reducing time of germination and enhanced germination and seedling emergence in primed brinjal seeds [113]. Kiran et al. [19] investigated the effect of different concentrations of NaCl in brinjal seeds. They reported controlled rehydration with 320 mM NaCl resulted in the increased enzymatic activities like catalase, superoxide dismutase, ascorbate peroxidase, glutathione reductase which scavenged ROS levels increased above the ‘oxidative window’ in the cells. It activated KU70 and MSH2 genes responsible for activation of non-homologous end joining (NHEJ) and mismatch repair (MMR) pathway respectively. KU70 gene functions in G1 phase of cell cycle and is involved in DNA replication. Higher levels of KU70 gene also arrests the cells in G1 phase extending the seed viability or initiate cell cycle during imbibition/rehydration reactivating the cells. Yalamalle et al. [114] reported 5-azacytidine (a DNA demethylating agent) treated onion seeds had increased total antioxidant capacity and the superoxide dismutase (SOD) activity. 5-azacytidine treatment enhanced seed germination, seedling length, seedling dry weight and seed vigour indices of aged onion seeds indicating probable role of DNA methylation during seed ageing. Though the influence of priming in seeds at gene levels cannot be ascertained, due to its reportage still in the preliminary stages.

Priming and agronomic bio-fortification

Priming as a technique holds great potential to serve as an economically feasible route for curbing present micronutrient deficiencies in the global food chain. Biofortification refers to the process of enriching nutritional quality of the food crops with higher vitamins, minerals and proteins *via* three strategies - agronomic biofortification, plant breeding approach and transgenic biofortification [115]. Seed priming with nutrients (nutripriming) aids the crop to meet its micronutrient requirements and improves germination, seedling emergence, stand establishment, yield, grain micronutrient quantity, resistance to abiotic and biotic stresses amidst changing environment and nutrient deficiencies in seeds using lesser nutrients than foliar spray and fertilizers though the standardisation of the best performing dose is a subject of genotoxic studies. Priming with metals such as Zn positively influences the seed progression from dormancy to germinating state. This can be possibly due to the role of BLUE MICROPYLAR END 3 (BME3), a GATA Zn finger transcription factor whose activity enables radicle protrusion without mechanical constraints, thereby enhancing germination parameters [116]. This can be correlated with observations of deeper dormancy in seeds with mutant BME3 [117]. Seed priming with zinc salts ($ZnSO_4$ and $ZnCl_2$) in sugar beet increased the Zn concentration, making it a potential biofortification candidate which could be correlated with the increase in photosynthetic rate, transpiration and stomatal conductance of the plant [118]. Similarly, marked improvements were reported in tomato growth, photosynthetic rate and stomatal conductance on seed priming with 10mg/L $FeSO_4.7H_2O$ with increased fruit Fe content, lycopene and β-carotene levels [119]. Additionally, engineered nanomaterials are currently being called into use to sustainably improve the efficiency of current agricultural practices and crop productivity by enhancing the agrochemical delivery efficiency to plants [120].

STORABILITY OF PRIMED SEEDS

Reduced seed storability or longevity is one side effect of primed seeds [121]. Primed seeds cannot be stored for longer duration of time especially under ambient conditions. Under the ambient storage conditions, viability, vigour and quality of seeds may decline making primed seeds less profitable. Primed seeds are stored at 4°C so as to slow down all the metabolic processes of the seeds to the least level. Primed seeds are physiologically more active in terms of the germination process as compared with seeds that have not been primed and thus primed seeds are more susceptible to deterioration [44]. The loss of longevity during priming is a disadvantage for commercial distribution of high-quality seeds. It has been observed that the cell cycle's advancement during priming is a crucial milestone that controls the capacity of seeds to be stored after the priming. Storability of seeds is also dependent upon several factors like storage temperature, packaging material, seed moisture content which play a major role in enhancing the seed longevity [122]. Tarquis and Bradford [123] used different priming methods in lettuce seeds, they found that primed seeds were more susceptible to degradation during storage than unprimed seeds. Zhang et al. [124] primed the seeds of brinjal and stored at 4°C for 1 month and then used for the germination test. They found that priming seeds with 3% KNO_3 solution supplemented with 0.1mM salicylic acid resulted in retention of beneficial effects of priming after being kept at 4°C for 30 days.

Cell cycle's advancement during priming is a crucial milestone that controls the capacity of seeds to be stored after the treatment. Cell cycle inhibitors impede or stop cell cycle progression, lowering the rate of cell division and the quantity of cells that are actively cycling at the cell stage depending upon the type of inhibitor selected and its underlying mechanism. *Arabidopsis* seeds primed with the cell cycle inhibitor mimosine outperformed other treatments [32]. A decline in seed viability and vigour is observed in naturally aged or accelerated aged and stored seeds. Various seed priming, coating, and combination treatments have reportedly increased metabolic activities, seed viability, and storability in stored seeds of cucumber [125], onion [126], carrot and leeks [127].

Chemical agents like cell cycle inhibitors can also be used as an effective priming treatment, arresting the highly synchronous cell cultures of seeds in the G1-S phase and hence enhancing the seed storability [32]. Although useful, these techniques have also been reported to have deleterious effects on germination percentage, speed of germination, and seed longevity [128,129]. Higher relative expression of genes governing biosynthesis of antioxidants and major hormonal genes can act as markers to measure seed longevity and viability at molecular level.

Priming with cell cycle inhibitors is known to enhance germination as well as longevity of seeds after treatment. Most commonly used cell cycle inhibitors are mimosine, aphidicolin, hydroxyurea and oryzalin. Mimosine has allelopathic effects and is an inhibitor of cell division, including the capacity to block the cell cycle before the G1/S transition [130,131]. Aphidocolin and hydroxyurea block the cell cycle at S phase of cell division. Oryzalin act after G2 phase or at M phase. The seeds after priming stored at controlled conditions (4°C) have more storability as compared to room temperature (25°C). Certain post-priming treatments are available to address this issue.

LIMITATIONS OF SEED PRIMING

Priming, though beneficial, is a technique not devoid of shortcomings. Seed longevity serves as a principle constraint of the primed seeds and is further aggravated by the combinational strains of seed quality, moisture levels and environmental conditions during storage like light, moisture, aeration, temperature and priming duration. Each priming strategy has its own set of benefits and drawbacks, as well as the potential for diverse outcomes. Proper environmental factors result in providing an ideal and safe environment to seed to attain its highest potential. Although economic, the research and development that goes into standardizing the priming agent, moisture levels and time duration most effective for a crop is a tedious and time-consuming process.

Another factor influencing the efficacy of priming is the duration of priming. The duration of the priming process varies depending upon the priming solution, temperature and osmotic potential of the solution. Ali et al. [132] reported that tomato seeds primed in a solution with an osmotic potential of -0.58 to -0.86 MPa germinated faster than those primed in a solution with an osmotic potential of -1.19 or -1.49 MPa. Singh et al. [133] found that celery seeds primed with PEG 6000 @ 300 g L^{-1} germinated faster than seeds primed with PEG 6000 @ 400 g L^{-1}.

There is also an added risk of microbial attack if primed for longer durations due to the lack of aeration. Aeration impacts seed respiration and viability that assists in germination and is a significant factor in offering a safer seed environment. Aerated PEG treated seeds resulted in higher germination and vigour indices than non-aerated PEG solution treatments [134,135]. Quality of light also influenced the primed seed characteristics. Nakamura et al. [136] found that priming of celery seeds under light produced more germination at high temperatures than priming in the dark.

Temperature is a significant component that influences seed germination. Radicle growth during priming may be inhibited if the soaking temperature is kept below the acceptable range. According to Basra et al. [137] the ideal temperature for most seed germination is between 15 and 30°C. Wahid et al. [138] showed that seed priming should be carried at temperatures ranging from 15 to 20°C with priming time ranging from nearly 8 hours to 14 days depending on plant species, osmotic potential, osmotic solution, and temperature.

Current priming agents like cell cycle inhibitors, plant growth regulators, pure botanical extracts and osmolytes are costly for a farmer. Commercial level priming of vegetable seeds prove to be expensive due to high input costs of both seeds and treatment pre-requisites. Proper storage facilities aid to the seed shelf life but also pose an additional economical barrier in the widespread use of the technique.

CONCLUSIONS AND FUTURE PROSPECTS

Horticulturists all around the world are undergoing increasing pressure constantly to catch up with the ever rising demand for more vegetable crops expected to rise up to $11.36 billion by 2028 as per market forecasts. Seed priming presents as an extremely useful technique to invigorate and enhance the quality of older seed lots, bringing them into commercial use, lowering the resource wastage and the fresh seed lot dependence every year. The benefits of seed priming have been well documented in terms of enhanced crop emergence, plant stand, yield, quality while reducing the susceptibility to biotic and abiotic stresses. Despite the benefits, there is still a major dearth in proper research and development within a farm based investigations. Primed seeds have lower storability and the longevity of seeds is heavily dependent on the genetic (initial seed quality) and environmental factors (like seed moisture content, relative humidity, temperature, and packaging material used for storage). It is therefore pertinent to study the effects of priming treatments on the germination, early seedling growth and storability of vegetable seeds so as to get a better understanding of the underlying mechanisms at molecular level and to analyse and measure gene expression levels of specific genes accurately to propose a particular priming treatment commercially. Biofortification of crops with micronutrients needs a deeper knowledge of physiological, biochemical and molecular mechanisms of their cellular activity and transportation. The regulation of proteins involved in nutrient accumulation should be studied at transcriptional and post translational level.

Also, very limited number of post-priming treatments are available to address the issue of reduced seed longevity after seed priming. Since, vegetable seeds are very expensive on the pockets of farmers and seed producers, innovative post priming treatments for storage should be the focal point of upcoming research. More novel chemicals like cell cycle inhibitors, 5-azacytidine (a DNA demethylating agent), etc should also be researched on a range of vegetable seeds for their effectiveness on germination and storability potential.

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