Seed Priming: Factors Affecting Efficacy

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Abstract

Seed vigor is the root of fast and uniform emergence and development of plants under variable environmental conditions. Biologists have investigated and developed several approaches to improve seed vigor and consequently plant establishment, including a seed invigoration technique known as seed priming. Seed priming is a pre-sowing treatment in which seeds are partially hydrated to a level that allows germination metabolic processes to initiate, sometimes accelerated by growth regulators, but seeds are held in the lag phase of germination thus preventing radical emergence. When primed seeds are sown, faster germination, greater synchronicity, improved seedling vigor and hence greater resistance to environmental stresses such as salinity and drought is often obtained. The most common forms of seed priming, based on the priming medium in which the seeds are soaked are hydropriming, halopriming, osmopriming and hormone priming. The implementation of these treatments may result in variable effects and harmful effects can result from inappropriate seed treatment. The desired effects of priming treatment are determined by several factors including plant species or variety, nature and concentration of priming medium, and length of soaking period. Variation in the efficacy of seed priming treatments between seed batches is a constraint to uptake of this technique. In order to facilitate a greater adoption of seed priming it will be necessary to develop more generic, safe priming protocols.

Keywords: *Halopriming, Hormopriming, Hydropriming, Osmopriming, Matrixpriming, Biopriming, Nutripriming.*

Introduction

Germination and early seedling establishment are crucial phases in the plant life cycle. Seed vigor is a significant feature that allows fast and uniform emergence and development under a range of environmental conditions (Ventura et al., 2012). Consequently, extensive research has been undertaken to improve seed vigor, viability and seedling establishment, particularly under salt and drought conditions, but also under normal unstressed conditions. To improve vigor, seeds are often exposed to pre-germination treatment, a process described as priming. This technique is also referred to as seed invigoration (Barsa et al., 2005; Bewley et al., 2013) or physiological seed treatment (Khan, 1992). There are several priming agents used, including, water, organic and inorganic salts, and plant growth regulators, and, based on the agent used, priming is classfied as hydropriming, halopriming, osmopriming, hormone priming, matrix priming, nutrient priming (nutripriming) or biopriming. The first four methods are the most commonly used, and this review paper focuses on them as well the factors that influence their effectiveness.

Priming is primarily a pre-sowing treatment in which water uptake is controlled so that sufficient uptake occurs to allow the germination metabolic processes to begin, but insufficient to enable the radical to emerge (Heydecker et al., 1973; Soeda et al., 2004; Ashraf & Foolad, 2005). Hormone priming, additionally, stimulates the early germination processes. In other words, the seeds are permitted and enabled to accomplish the early metabolic events of germination but with the prevention of radical protrusion so that the seeds are held in the lag phase of germination (Taylor et al., 1998). Radical emergence is prevented by the water potential of the priming agents or by drying back the seeds to maintain a critical water content. Furthermore, based on the fact that the seeds of the majority of plant species are desiccation-tolerant, primed seeds can be dried back to their original weight prior to protrusion of the radical (Hilhorst et al., 2010) and stored before later use (Ashraf & Foolad, 2005).

This biological approach to improving crop establishment has been widely utilized owing to its beneficial effects, including enhancement of germination percentage and germination rate, greater uniformity of growth, and improvement of plant growth and yield, particularly under harsh environmental conditions such as salt, drought and temperature stresses (Halmer, 2004; Nascimento & De Aragão, 2004; Ashraf et al., 2008; Patade et al., 2009). It has also been reported that seed priming may induce early ripeness and greater pest tolerance in field crops (Harris et al., 1999). In addition, priming has been considered a simple, economical, low risk approach (Ashraf & Foolad, 2005).

Hydropriming

Hydropriming is the process in which seeds are soaked in water prior to sowing. With this technique, treated seeds can be used directly after soaking or exposed to one or more cycles of hydration and dehydration (Barsa et al., 2005; Farooq et al., 2004; Farooq, Barsa, Khalid, et al. 2006; Farooq, Barsa, Tabassum, et al. 2006; Farooq et al., 2007). In the case where hydroprimed seeds are dried, the treated seeds are often dried back approximately to their original weight (Rehman et al., 1998; Andoha & Kobata, 2001; Demir & Mavi, 2004, Rouhi et al., 2011; Azra et al., 2013). In addition, when this is the case, it is referred to as hardening (Rehman et al., 1998; Andoha & Kobata, 2001). Furthermore, this approach is also described by Harris (1992), Harris (2004) and Harris et al. (1999) as on-farm seed priming. Moreover, it has been claimed that hydropriming is environmentally friendly as the waste products of osmopriming or matrixpriming are avoided (Halmer, 2004).

Harris (2004) reported that hydropriming of several crops has proved effective in countries such as India, Nepal, and Pakistan, and is considered to be simple and to have no risks. It has been found that hydropriming significantly increased the germination capacity and the germination rate of maize (*Zea mays*) seeds compared with unprimed seed (Tian et al., 2014) as well as improving seedling establishment of lentil (*Lens culinaris*) (Ghassemi-Golezanik et al., 2008). Moreover, hydropriming has also been reported to be an effective treatment in enhancing the germination percentage, germination index, energy of emergence, and the growth of maize seeds (Kumari et al., 2017), *Gerbera jamesonii* (Ahmad et al., 2017), wheat (*Triticum aestivum*) (Azra et al., 2013), and a number of vegetable crops including tomato (*Solanum lycopersicum*), onion (*Allium cepa*), watermelon (*Citrullus citrullus*) and chilli (*Capsicum annuum*) (Maiti et al., 2011). Beneficial effects of hydropriming have also been reported by Dezfuli et al. (2008) and Afzal et al. (2004). Similarly, hydropriming was also found to be effective in improving the germination percentage and/ or rate of several forest trees such as black spruce (*Picea mariana*) (Malek, 1992), amendiom bravo (*Pterogyne nitens*) (Biruel et al., 2007), *Acacia nilotica* (Umarani et al., 1999) and *Acacia cyanophylla* (Eshkab et al., 2014).

The performance of plants exposed to salt stress was considerably improved by hydropriming (Ashraf & Rauf, 2001; Cassaro-Silva, 2002; Barsa et al. 2005; Afzal, Barsa, Hameed, et al. 2006; Afzal, Barsa, Ahmad, et al. 2007; Naeem & Muhammad, 2006; Neamatollahi et al., 2009; Abbasdokht, 2011; Akter et al., 2018; Oliveira et al., 2019). Under saline conditions, the yield of barley (*Hordeum vulgare*) was significantly increased by hydropriming (Rashid et al., 2006). Furthermore, the technique also enhanced the drought tolerance of sesame (*Sesamum indicum*) seeds (Morteza et al., 2017), as well as the disease resistance of pearl millet (*Pennisetum glaucum*) (Harris et al., 2005) and the storagability of low vigor wild cabbage (*Brassica oleracea*) seeds (Powell et al., 2000).

Osmopriming

Osmopriming or osmoconditioning is a term describing the soaking of seeds in an osmotic solution, which permits the seeds to hydrate but prevents the extension of the radical through the seed coat. Polyethylene glycol (PEG), glycerol and mannitol are among the agents used for osmopriming. Whilst soaking in an osmoticum, some of the seed's biochemical and physiological processes are started, but the organic compounds used to lower the water potential of the soaking solution do not penetrate into the treated seeds (Khan, 1992). For exasmple, the large molecular size of PEG prevents its uptake into the embryo and, consequently, its toxic effect is avoided (Di Girolamo & Barbanti, 2012). Therefore, it is one of the most widely used osmotica (Lemmens et al., 2019). However, PEG can prevent oxygen mobility and thus it is essential to aerate seeds while soaking in PEG (Mexal et al., 1975; Paparella et al., 2015).

Osmopriming is important in enhancing both germination and the performance of crops under normal or saline conditions. For instance, PEG has been reported to increase the germination and seedling vigor of wheat (Salehzade et al., 2009; Faijunnahar et al., 2017) and of tomato (Asgharipour et al., 2014). The beneficial effects of osmopriming with PEG on the germinability and yield of grain of two wheat cultivars, namely, Adana-99 and Pandas were also reported by Toklu et al. (2015), and Faijunnahar et al. (2017). Similarly, osmopriming with PEG significantly increased the final germination and/or germination rate of canola (*Brassica napus*) cv. Zafar-2000 (Afzal et al., 2004) and of maize (Tian et al., 2014) compared with unprimed seeds.

Moreover, osmopriming with PEG has also proved effective in ameliorating the adverse impact of salinity on maize (Akter et al., 2018), sorghum (*Sorghum bicolor*) (Haghighat et al., 2012) and wheat (Ghiyasi et al., 2008). PEG has also effectively enhanced the drought tolerance of sesame seeds (Morteza et al., 2017). Tanne and Cantliffe (1989) also reported that PEG effectively enhanced the germination percentage and germination rate of celery (*Apium graveolens*) seeds under high temperature. The beneficial effects of PEG on the germination percentage and rate of *Viola* × *wittrockiana* under different incubation temperatures were also found by Szopińska et al. (2014). PEG has also proved effective in overcoming dormancy of tomato seeds (Farooq, Barsa, Saleem, et al. 2005).

Halopriming

This is a term used when seeds are soaked in inorganic salts such as NaCl, KCl, $CaCl_2$, $MgSO_4$ or KNO_3. In order to gain the beneficial influence of priming, seeds are soaked in a salt solution of which the osmotic potential has been adjusted to enable the treated seeds to begin a number of physiological and chemical phenomena but at which radical emergence is prevented (Khan, 1992). However, the type and osmotic potential of the priming agent and soaking period are very significant parameters that determine their effectiveness (Ashraf & Foolad, 2005; Abdulrahmani et al., 2007).

Halopriming was found to be effective in improving the seed performance and seedling vigour of rice (*Oryza sativa*) grown under normal conditions (Farooq, Barsa, Khalid, et al. 2006), watermelon (Demir & Mavi, 2004) and maize (Kumari et al. 2017). It has been reported that $CaCl_2$ successfully improved the germination rate, uniformity and seedling vigour of rice (Farooq et al., 2007), and seed vigour of gerbera daisy (*Gerbera jamesonii*) and zinnia (*Zinnia elegans*) (Ahmad et al., 2017). The beneficial effetcs of NaCl as a priming agent have also been reported with many plants such as maize (Abraha & Yohannes, 2013; Tian et al., 2014), lemon balm (*Melissa officinalis*) (Younesi & Moradi, 2015) and three varieties of green gram (*Vigna radiata*) (Jisha & Puthur, 2014). Similarly, halopriming with KNO_3 was found to be beneficial in enhancing the germination rate of tomato seeds (Lara et al., 2014) and germinability of solid bamboo

(*Dendrocalamus strictus*) (Kumar et al., 2020). KNO_3 beneficially enhanced the emergence, uniformity and seedling growth of endive (*Cichorium endivia*) and chicory (*Cichorium intybus*) in nurseries and greenhouses (Tzortzakis, 2009). In addition, Mavi et al. (2006) concluded that this agent was superior to other priming agents in increasing the germination percentage, germination rate, and fresh and dry weight of two tomato cultivars compared with unprimed seeds. Moreover, halopriming also resulted in dormancy breaking of tomato seeds (Farooq, Barsa, Saleem, et al., 2005), enhancement of germination of low vigour seeds of Japanese cedar (Kim et al., 2008), and reduction in the incidence of seedling damping off in beetroot (*Beta vulgaris*) (Osburn & Schroth, 1988).

Halopriming has proven to be effective in mitigating the profound impact of salinity. The ameliorating effect of halopriming with NaCl on the performance of a number of crops under saline conditions has been widely reported. For instance, NaCl significantly improved the germination rate and/or germinability of sorghum (Haghighat et al., 2012), sugarcane (*Saccharum officinarum*) cultivars (Patade et al., 2009), maize (Akter et al., 2018), perennial rye (*Secale cereanum*) (Shahri et al., 2015), and the emergence percentage and emergence rate of hot pepper cv. Hot Queen (Amjad et al., 2007). This agent also effectively enhanced the growth and/or seedling vigor of three *Vigna radiate* varieties (Jisha & Puthur, 2014), four cultivars of coriander (*Coriandrum sativum*) (Ben Fredj et al., 2014), hot pepper cv. Hot Queen (Amjad et al., 2007), chicory (Hossein & Robati, 2015) and two melon (*Cucumis melo*) cultivars (Sivritepe et al., 2003; Sivritepe et al., 2005). Moreover, NaCl resulted in the enhancement of the drought tolerance of sesame seeds (Morteza et al., 2017).

Halopriming with $CaCl_2$ also resulted in increased salt tolerance of wheat (Afzal, Barsa, Hameed, et al., 2006; Afzal et al., 2008; Rafiq *et* al., 2006; Azra et al., 2013; Feghhenabi et al., 2020), cowpea seeds (Farooq et al., 2020) and the performance of chickpea (*Cicer arietinum*) seeds under chilling stress (Farooq et al., 2017). The profound impact of salt stress on sunflower (Kaya et al., 2006; Bajehbaj, 2010) and melon cv. Gaúcho Casca de Carvalho Comprido) (Oliveira et al., 2019) was alleviated by treating their seeds with KNO_3.

Hormone priming

Hormone priming describes soaking seeds in plant growth regulators (PRGs) such as gibberellic acid (GA_3), indole acetic acid (IAA), indole butyric acid (IBA), kinetin, ascorbic acid (AA), salicylic acid (SA) and maleic hydrazide (MH). Many-studies have shown that priming with plant growth regulators enhances the germination and growth of various species of plants (Ashraf & Foolad, 2005). For instance, it has been reported that 500 ppm GA_3 remarkably improved the germination percentage, germination rate, and fresh and dry weight of two tomato cultivars (Mavi et al., 2006). The germination capacity of two varieties of cowpea (*Vigna unguiculata* L.) was significantly increased by soaking in 5 or 10 ppm IAA, GA_3 or AA (Audi et al., 2009). Pre-treating the seeds of maize in 100 ppm GA_3, SA or AA resulted in significant enhancement of germination percentage, germination index, energy of emergence, seedling growth and vigor indices (Kumari et al., 2017). Similarly, the beneficial effects of three concentrations of GA_3 on the final germination and germination rate of maize seeds were reported by Tian et al. (2014). Ma et al. (2018) also found that 5, 10, 50, 100 or 200 μM GA_3 considerably improved the germination rate and plant height, and fresh and dry weight of shoots of Chinese lyme grass compared with unprimed seedlings. Hafeez ur Rehman et al. (2015) also found that hormone priming with SA significantly decreased mean time of emergence and membrane permeability, and improved emergence rate, emergence index and seedling vigor of early planted spring maize

It has also been concluded that hormone priming significantly improved the salt tolerance of a number of crops including wheat (Balki & Padole, 1982; Afzal, Barsa, Ahmad, et al., 2005; Afzal, Barsa, et al. 2005; Afzal, Barsa, Farooq, et al. 2006; Iqbal & Ashraf, 2006; Akbari et al., 2007; Hamid et al., 2008; Iqbal & Ashraf, 2013), sugar beet (*Beta vulgaris*) (Jamil & Rha, 2007), *Melissa officinalis* (Younesi, & Moradi, 2015) and barley (Naeem & Muhammad, 2006). Moreover, the drought tolerance of rape seeds (*Brassica* *napus var. napus*) was considerably improved by treating them with GA_3 and melatonin (MT) (Khan et al., 2020). Similarly, it has been reported that priming seeds with AA enhanced the early seedling growth of alfalfa (*Medicago sativa*) (Salemi et al., 2019), and the germination percentage and seedling growth of chicory seeds under drought stress (Hossein & Robati, 2015). In addition, hormone priming with 0.09 mM IAA and 1.0 mM SA significantly alleviated the adverse impact of *Orobanche ramosa* stress on tomato especially at oxidative stress levels (Madany et al., 2020). Salicylic acid as priming medium with brinjal (*Solanum melongena*) seeds has also proved effective in enhancing germination and seedling vigor, and resistance to wilt caused by *Verticillium dahliae* (Mahesh et al., 2017). The same agent has significantly enhanced resistance of thyme (*Thymus vulgaris*) seeds to contamination stress generated by cadmium (Cd) (Moori & Ahmadi-Lahijani, 2020). However, Maiti et al. (2006) claimed that seed priming with PGRs is inconvenient and expensive for poor farmers and the technique is not easy to use.

Nutrient priming

Nutrient priming or nutripriming refers to imbibition of seeds in nutrient solutions rather than pure water. This technique has been developed to enhance the nutrient content of seeds as well as priming them to increase seed and seedling vigor (Farooq et al., 2012; Muhammad et al., 2017; Nauman et al., 2018). With this technique, both micro and macro nutrients can be used (Rehman et al., 2012; Farooq et al., 2019). However, micronutrients are the most commonly used as nutrient priming agents. Micronutrients play vital roles in respiration and photosynthesis of plant physiological processes (Marschner, 1995). According to Johnson et al. (2005) soil fertilizer, foliar sprays and seed treatment are three methods of applying micronutrients to plants. The first two methods are the most commonly practised in agriculture. However, they are unaffordable for poor farmers who may also face difficulties in obtaining high quality micronutrients. Therefore, micronutrient seed treatment provides an easy and cost effective technique to enhance crop micronutrient status.

Seed nutrient priming can enhance seedling emergence and establishment of stands, ensuing development and yield. For instance, Abbas et al. (2014) found that priming two rice seed cultivars with 0.1 or 0.5% zinc (Zn) solution increased the germination percentage, germination rate, germination vigor, and germination index. However, 1% Zn was found toxic to both seed cultivars. It has also been reported that nutrient priming of maize seeds with 1% phosphorus (P) derived from KH_2PO_4 resulted in significant improvement of cob yield, plant height, number of grains per cob, grain weight, straw yield , and grain P content compared with the control. The enhancement percentage of these parameters was 127, 87, 26, 157, 94 and 44%, respectively of unprimed seedling (Miraj et al., 2013). Similarly, priming of two wheat seed cultivars with 0.001% boron (B) proved effective in improving stand uniformity and early seedling growth. However, 0.1% adversely influenced the germination and seedling growth (Iqbal et al., 2012).

Farooq et al. (2011) also found that 0.001 or 0.1% B enhanced the germination capacity, germination energy, germination rate and germination index of rice seeds cv. Super Basmati. However, 0.5% B entirely suppressed germination and growth. Moreover, treating wheat seeds (cv. Faisalabad-2008) with 0.5M Zn, 0.1M B, 0.1M manganese (Mn) or with combinations of these elements effectively enhanced stand establishment, grain yield, and straw and grain micronutrient contents. However, a combination of Zn+B was the most effective treatment (Nauman et al., 2018). In addition, several reports indicate the potential of nutrient priming in enhancing the performance of several crops under stress conditions such as salinity (Shahverdi et al., 2017; Imran et al., 2018), drought (Nawaz et al., 2012; Begum et al., 2014), low root zone temperature (Imran et al., 2013) and Zn deficiency (Nautiyal & Shukla, 2013; Muhammad et al., 2017).

Biopriming

Biopriming refers to hydrating seeds in a solution containing beneficial microorganisms such as *Trichoderma harzianum*, *T. viride*, *Pseudomonas flourescens*, *P. putida*, *P. aeruginosa*, *Bacillus lentus*, *B. subtilis*, *Azospirillum lipoferum* and *Azotobacter chroococcum*. Seed imbibition in bacterial suspensions allows the germination metabolic processes to begin but can be halted before radical emerge occurs (Anitha et al., 2013). Beside the beneficial effects that can be gained through other priming techniques, biopriming provides protection of seeds against soil- and seed-borne diseases (Reddy, 2013; Mona et al., 2017).

Several studies indicated the potential of biopriming in improving a number of agronomic indices and disease resistance for number of crops. For instance, Ananthi et al. (2014) investigated the effects of different durations of hydropriming, and different concentrations and soaking duration of biopriming with *T. viride* or *P. fluorescens* on chilli seeds. Soaking in 60% *T. viride* for 3h or 60% *P. fluorescens* for 12h were the most effective treatments in improving the germination percentage, germination rate, seedling growth and seedling vigor index compared with an unprimed control.

Basavaraj et al. (2019) reported that biopriming of pearl millet with *P. fluorescens* or *T. virens* enhanced germination capacity and seedling vigor. They also found that both biotic agents significantly increased resistance against blast disease caused by *Magnaporthe grisea*. However, *P. fluorescens* was the more effective. Similarly, Forti et al. (2020) concluded that biopriming of barrel medic (*Medicago truncatula*) seeds with *B. spp* is effective in increasing seed germination and seedling establishment in contaminated soils. The growth of maize, as well as its disease resistance against *Rhizoctonia solani* MF-30, which causes banded leaf and sheath blight, were significantly higher with *P. aeruginosa* primed seeds than with unprimed ones (Singh et al., 2020) *Trichoderma harzianum*, *T. viride*, *B. subtilus* and *P. flouresens* as biopriming agents of soybean seeds considerably increased the plant height, root and shoot fresh and dry weight, number of branches, yield parameters, and resistance against root rot disease as well as seedling protection against soil borne infection (Mona et al., 2017).

Solid matrix priming

Solid matrix priming, which is also known as a matrix conditioning, is proposed to avoid the high cost and technical issues associated with osmopriming media (Paparella et al., 2015). In this technique seeds are incubated in a solid insoluble matrix for a given time. After treatment, seeds are removed from the matrix followed by washing and drying them back. Solid insoluble matrices include vermiculite, peat moss, charcoal, sand and clay (Mondal & Bose, 2014). For effective solid matrix priming, high water holding capacity, low matrix potential, minimum water solubility, lack of toxicity to seeds, and adherence to the seed coat are all desirable characteristics (Di Girolamo & Barbanti, 2012; Paparella et al., 2015). In addition, the chemical composition and pH of the carrier significantly influenced the performance of seeds (Harman & Taylor, 1988).

Effectiveness of solid matrix priming has been demonstrated for many crops. For instance, perlite as a solid matrix used to prime high and low (artificially aged) vigor seeds of bitter gourd (*Momordica charantia*) cv. Solan Hara significantly enhanced emergence and fruit yield. However, low vigor seeds showed a greater response to priming (Kanwar & Mehta, 2017). The beneficial effects of solid matrix priming of seeds with ground Leonardite shale on the germination rate measured by reduction in T50% and gain in dry weight of tomato, carrot (*Daucus carota*) and onion was also reported by Taylor et al. (1988). Moreover, Mereddy et al. (2000) reported that seven out of ten solid matrix agents significantly improved the seed vigor of okra (*Abelmoschus esculentus*) seeds. However, long priming times resulted in lower germination and vigor indices due to growth of fungi. Calcium aluminium silicate primed seeds of okra showed considerable enhancement in the final germination, seedling vigor and fruit yield (Sharma et al., 2013). Matrix priming with vermiculite also improved the germination percentage and decreased mean time of germination and ion leakage of leek (*Allium ampeloprasum*) seeds (Ozden et al., 2018).

Matrix priming also proved effective in enhancing the performance of crops exposed to stress conditions. For example, vermiculite as a priming agent enhanced the germination vigor, germination index and vitality index of broccoli (*Brassica oleracea* var. italica) and cauliflower (*B. oleracea* var. botrytis) seeds grown under salt stress conditions (Wu et al., 2019). Matrix priming combined with *T. viride* effectively increased field emergence of okra seeds under optimum (15°C) and suboptimum (25°C) temperatures compared with hydropriming and untreated seeds (Pandita et al., 2010). Likewise, priming seeds of celery with 10 g calcined clay resulted in remarkable improvement in the germination at high temperature (Pareraet al., 1993). In addition, matrix priming also effectively reduced the time needed to break dormancy of seeds of Pacific silver fir (*Abies amabilis*), subalpine fir (*A. lasiocarpa*), grand fir (*A. grandis*) and noble fir (*A. procera*) (Ma et al., 2003). Effectiveness of matrix priming in breaking dormancy of lettuce (*Lactuca sativa*) was also reported by Taylor et al. (1988).

Factors Influencing the Response of Seeds to Priming

The beneficial effects of pre-sowing seed treatments have been widely reported; however, in some cases priming did not induce the expected beneficial effects or was even disadvantageous. For example, reduction in germination due to priming was reported with seeds of barley **(**Abdulrahmani et al., 2007), cowpea (*Vigna sinensis*), (Ogbonna & Abraham, 1989), wheat (Giri & Schillinger, 2003), maize (Ghodrat & Rousta, 2012), palisade grass (*Brachiaria brizantha*) (Amorim et al., 2015) and tomato (Asgharipour et al., 2014). Moreover, germination inhibition because of priming was also reported with rice (Farooq, Barsa, Hafeez, et al. 2005; Farooq, Barsa, Hefeez-ue-Rehman, et al. 2006).

Plant species or varieties, type and water potential of the priming agent, and duration of soaking are all reported to be factors influencing the effects of priming (Geetha et al., 1997; Afzal et al., 2004; Ashraf & Foolad, 2005; Abdulrahmani et al., 2007). Seed quality has also been claimed to influence the outcome of priming (Powell et al., 2000; Podlaski et al., 2003; Halmer, 2004; Nascimento & De Aragào, 2004).

1- The Effect of Priming Agents

Irrespective of concentration, there are many priming agents that can be used, but their efficacy varies and hence there may be a specific agent preferred for a given species or cultivar, making it difficult to formulate general recommendations. Afzal et al. (2008) studied the effect of three halopriming agents on the growth of wheat under saline conditions and they concluded that $CaCl_2$ or $CaSO_4$ were more effective than NaCl as a priming agent in decreasing the adverse impact of salinity on the growth of wheat. The effect of three priming agents namely, halopriming with KNO_3 or NaCl, or osmopriming with PEG 8000 on four tomato cultivars was studied by Farooq, Barsa, Saleem, et al. (2005). The results showed that all priming agents effectively increased the final germination, germination rate and seedling vigor compared with unprimed seeds. However, KNO_3 was more effective than the other agents.

Afzal et al. (2012) elucidated the effect of seed priming on the salt tolerance of two rice cultivars, Shaheen Basmati and Basmati-2000. The seeds were soaked for 36 h in distilled water or in 2.2% $CaCl_2$, KCl or 50 mM H_2O_2. The results indicated that $CaCl_2$ was the most effective agent in enhancing the salt tolerance of both cultivars as indicated by increased germination capacity, germination rate and seedling growth. In addition, an adverse impact of H_2O_2 on the germination rate and seedling growth of both cultivars was observed. Shahverdi et al. (2017) studied the effects of nutripriming agents on the salt tolerance of stevia (*Stevia rebuadiana*) seeds. The seeds were treated with selenium (Se), iron (Fe), boron (B) or combinations of B+ Fe, Fe + Se, Se + B or Fe + B + Se. Under both normal and salt stress conditions, the highest final germination, germination rate, germination value and seedling vigor index were recorded in seeds treated with Fe + B. Yari et al. (2010) also concluded that hydropriming was more effective than halopriming or osmopriming in increasing the speed of germination of seeds of two wheat cultivars. Similarly, although hydropriming or -2 bar of NaCl, or PEG 6000 improved the measured germination indices of sesame seeds compared with untreated seeds under normal and drought stress conditions, osmopriming with PEG for 16 h was the most effective treatment (Morteza et al., 2017). An experiment on the effect of hydropriming, hormone priming with 100 ppm GA_3, SA, or AA, and halopriming with 1% KNO_3 or $CaCl_2$ on maize seeds was conducted by Kumari et al. (2017). All priming media significantly improved germination percentage, germination index, energy of emergence, seedling length, seedling fresh weight and dry weight, and vigor indices. However, GA_3 was the most effective.

An investigation of the effects halopriming with 5 g l^{-1} KNO_3 or hydropriming on the salt tolerance of melon cv. Gaúcho Casca de Carvalho Comprido seeds was carried out by Oliveira et al. (2019). Primed and unprimed seeds were germinated under two levels of NaCl (–0.30 and –0.60 MPa). The results showed that both hydropriming and halopriming increased the germination capacity and germination rate index, reduced mean germination time, and enhanced early seedling growth under salt stress conditions compared with unprimed seeds. However, hydropriming was more effective than halopriming with KNO_3. In addition, Mavi et al. (2006) noticed that although 500 ppm GA_3, 2% KNO_3 or 1% NaCl as priming media significantly increased the germination percentage, germination rate, and fresh and dry weight of two tomato cultivars compared with unprimed seeds, KNO_3 was superior to the other treatments. It has also been concluded that while hydropriming significantly improved the total germination, germination rate, germination index, and vigor index of maize inbred line MO17, osmopriming with -1.2 MPa urea solution decreased the germination percentage and vigor index compared with unprimed seeds (Dezfuli et al., 2008). Furthermore, Toklu et al. (2015) reported the response of seeds of two bread wheat cultivars, namely Adana-99 and Pandas, to hydropriming, 100 ppm IAA, 2.5% KCl, 1% KH_2PO_4, 10% PEG-6000, or 100 ppm GA_3. After soaking, the seeds were dried back to their original weight. They found that PEG, KCl, and hydropriming were the most effective treatments in enhancing the germination capacity and yield of grain. Lara et al. (2014) also concluded that KNO_3 was superior to PEG in enhancing the germination rate and decreasing the mean germination time of tomato seeds. Similarly, different effects of priming agents on the salt tolerance of maize and sorghum seeds were also reported by Akter et al. (2018) and Haghighat et al. (2012), respectively. Likewise, Eshkab et al. (2015) also reported that although 10 mmol KCl, NaCl and CaCl2 effectively improved the final germination percentage, mean germination rate and coefficient velocity of the germination, germination index and germination rate index of *Acacia cyanophylla* seeds compared with untreated seeds, KCl proved most effective.

2- The Effect of the Priming Agent Concentration

The concentration or the osmotic potential of the priming agent is also a critical factor. Regardless of halopriming or osmopriming agent, a wide range of concentrations has been used. With halopriming, many salts and concentrations have been utilized. For example, seeds of many species have been treated with different concentrations of NaCl including 35 mM (Jisha & Puthur, 2014), 40 mM (Haghighat et al., 2012), 50 mM (Jisha & Puthur, 2014), 4 g l^{-1} (68.5 mM) (Ben Fredj et al., 2014), 100 mM (Patade et al., 2009), 1% (171 mM) (Mavi et al., 2006; Amjad et al., 2007), 197 mM (Sivritepe et al., 2003; Sivritepe et al., 2005), 50, 150 or 250 mM NaCl (Tian et al., 2014) and 280 mM (Farooq, Barsa, Saleem, et al. 2005).

Similarly, different osmopriming agents and concentrations have been used. For instance, concentrations of PEG (the most commonly used media) tested have included -1.0 MPa PEG-800 (Szopińska et al., 2014), -1.25 MPa PEG-8000 (Amjad et al., 2007), -0.3, -0.6, -0.9, -1.2, or -1.8 MPa PEG-8000 (Lemmens, 2019), -0.1, -0.2, -0.3, -0.4, -0.5, -0.7, -0.9, -1.1, -1.5 and 1.8 MPa PEG-8000 (Khalil et al., 2001), -0.2 MPa PEG-6000 (Morteza et al., 2017), -0.4, -0.8 or -1.2 MPa PEG-6000 (Asgharipour et al., 2014), -1.0 and -1.5 MPa PEG-6000 (Kuppusamy & Ranganathan, 2014), 10% PEG-6000 (Toklu et al., 2015) and 5, 10, 15 or 20% (Tian et al., 2014; Faijunnahar et al., 2017).

Variable concentrations of hormone priming media have also been used. For instance, concentrations of GA_3 used to prime seeds of many species include 1.5, 2.5 and 5 mg l^{-1} (Ghodrat & Rousta, 2012), 20 mg l^{-1} (Younesi & Moradi, 2015), 100, 150 or 200 mg l^{-1} (Iqbal & Ashraf, 2013), 5 or 10 mg $l^{-1\ 1}$ (Audi et al., 2009), 20 or 60 mg l^{-1} (Naeem & Muhammad, 2006), 100 mg l^{-1} (Kumari et al. 2017) and 500 mg l^{-1} (Mavi et al., 2006).

Clearly, while the required effects of the priming media might be obtained at specific concentrations or within a range of concentrations of a given agent, some concentrations may induce undesired consequences including germination reduction or even germination inhibition. There are many studies showing that some concentrations of a given agent may induce better results than others. For example, Ahmad et al. (2017) studied the effect of 25, 50 or 100 mM $CaCl_2$, KNO_3 or KCl and hydropriming on gerbera daisy and zinnia seeds. In regard to halopriming, the results revealed that except the germination capacity of zinnia seeds, all treatments significantly enhanced seed vigor as reflected by increased germination percentage, root and shoot length, seedling fresh and dry weight, and reduction in mean germination time and $T_{50\%}$.. However, 25 mM $CaCl_2$ was the most effective treatment for gerbera, whereas 50 mM $CaCl_2$ was the best treatment for *Zinnia elegans*. Moreover, Atia et al. (2006) also reported that 300 mM NaCl as a priming agent was more effective than 5 mM in enhancing the germination of rock samphire (*Crithmum maritimum* L.) in both normal and salt stress conditions. Similarly, 30 mM $CaSO_4$ was found to be more effective than 10 mM in enhancing the germination capacity of barley grown under salt stress conditions (Naeem & Muhammad, 2006). In addition, 15 or 200 mg l^{-1} of GA_3 were found to be more efficient than 100 mg l^{-1} in enhancing both the germination percentage and germination rate of salt stressed sugar beet seeds compared with the control (Jamil & Rha, 2007).

It has been observed that treating the seeds of Chinese lyme grass (*Leymus chinensis*) with 0.005, 0.01, 0.05, 0.1 or 0.2 mg l^{-1} GA_3 significantly improved the final germination, plant height and fresh and dry weight of shoots compared with unprimed seedlings. However, 0.05 mg l^{-1} was the most effective concentration (Ma et al., 2018). Likewise, the results of an experiment conducted by Iqbal and Ashraf (2013) showed that 150 mg l^{-1} GA_3 was more effective than 200 mg l^{-1} in mitigating the profound impact of salinity on the grain yield of two wheat cultivars. Gill and Al-Shankiti (2015) also concluded that the germination percentage, coefficient of rate of germination, accumulated speed of germination, number of leaves and shoot and root length of *Prosopis cineraria* seeds primed with 0.5 or 1% fulvic acid were considerably higher than that of untreated seeds. However, 1% was more effective. Similarly, Mahdavi and Rahimi (2013) found that although 0.05, 0.1, 0,2 and 0.5% chitosan remarkably enhanced the total germination and germination rate of ajowan (*Carum copticum*) seeds compared with unprimed seeds, the maximum effect was recorded at 0.2%. It has also been reported that 0.1 mM sodium nitroprusside was more effective than 0.2 mM in enhancing the salt tolerance of four wheat cultivars (Qasim et al., 2017).

It has been observed in many studies that, while some concentrations of priming agents effectively induced the desired effects, other concentrations of the same medium were not effective. For instance, Afzal, Barsa, Lodhi, et al. (2007) studied the effect of halopriming with 10, 25 or 50 mM NaCl or $CaCl_2.H_2O$ on wheat cv. Auqab-2000 under saline conditions. The results showed that most priming treatments were not effective in improving germination and seedling vigour under salt stress. However, priming seeds with 25 or 50 mM $CaCl_2.H_2O$ significantly reduced the mean germination time and significantly increased the shoot length, and fresh and dry weight of seedlings. Shahri et al. (2015) found that while soaking the seeds of perennial rye in 125 mM NaCl for 24 h effectively increased the germination percentage under 100 and 200 mM NaCl stress compared with untreated seeds, priming seeds for the same period in 250 or 500 mM NaCl failed to do so. Similarly, the results of an investigation conducted by Tian et al. (2014) indicated that while 10 or 15% PEG significantly increased the germination rate of maize seeds, 20% decreased it to a level equal to unprimed seeds.

Although, the beneficial effect of priming has been widely reported for many crops and tree species, undesired results have also been found. For instance, Abdulrahmani et al. (2007) observed that while 10 mM Zn did not affect the germination capacity and germination rate of barley seeds, a reduction in these parameters was observed in seeds treaed with 50 or 100 mM. Reduction in the germination rate of wheat seeds primed with 25 mM $Ca(NO_3)_2$, 50 mM NaCl or 100 mM $CaCl_2$ was also reported by Barsa et al. (2005). Likewise, the germination percentage of perennial rye seeds primed with 125, 150 or 250 mM NaCl was reduced in distilled water. The germinability was 56, 45 and 17%, respectively, compared with 99% recorded in unprimed seeds (Shahri et al., 2015).

Ghodrat and Rousta (2012) observed that the germination percentage and germination rate of maize seeds osmoprimed with 1.5, 2.5 or 5 mg l^{-1} GA_3 was significantly lower under both normal and saline conditions compared with unprimed seeds. They also found that both indices were severely decreased with increasing levels of the priming agent. The results of Shahverdi et al. (2017) showed that the germination capcity of B primed seeds of stevia (*Stevia rebuadiana*) at 0, 30 and 60 mM NaCl was statistically similar to untreated seeds. However, it was significantly reduced at 90 mM NaCl compared with uprimed seeds. Similarly, Arin et al. (2011) found that halopriming onion cv. Alix seeds with 2 or 4% KNO_3, KH_2PO_4 or -0.5, -0.1 or -1.5 MPa PEG resulted in significant reduction in the emergence percentage at 20ºC compared with unprimed seeds. They also observed that while no halopriming treatments affected the emergence rate of this cultivar, all concentrations of PEG decreased the emergence rate compared with untreated seeds. Moreover, although -0.4, -0.8 or -0.12 MPa PEG significantly improved the germination rate, and shoot and root length of tomato seeds compared with unprimed seeds, increasing the osmotic potential above -0.4 MPa resulted in significant reduction of root length (Asgharipour et al., 2014).

Germination inhibition due to seed priming has also been observed. For example, Farooq, Barsa, Hefeez-ue-Rehman, et al. (2006) elucidated the effect of 1, 5, 10 and 15% (v/v) aerated solution of ethanol on the possible invigoration of fine rice (Super-Basmati) seed. The seeds were soaked in the priming solution for 42 h followed by drying them back close to their original weight. The results showed that while none of the tested concentration improved the germination capacity compared with unprimed seeds, 10 and 15% entirely inhibited the germination and emergence of the examined crop. Similarly, complete inhibition of the germination of durum wheat (*Triticum durum*) seeds osmoprimed with -1.2 and -1.8 MPa PEG compared with 96% germination of unprimed seeds was reported by Lemmens et al. (2019). Likewise, Farooq et al. (2011) showed that 0.5% B entirely suppressed the germination and growth of rice (Super Basmati) seeds. However, beneficial effect on the germination capacity, germination energy, germination rate and germination index was obtained with 0.001 or 0.1% of the same agent. Germination and emergence inhibition of both fine and coarse rice due to osmopriming with 5% urea was also reported by Farooq, Barsa, Hafeez, et al. (2005). Moreover, Iqbal et al. (2012) also concluded that while 0.001% B proved effective in improving stand uniformity and early seedling growth of two wheat cultivars, 0.1% of this element adversely influenced the germination and seedling growth.

3- The effect of soaking duration

The duration of soaking of seeds in the priming agents has been claimed to interact significantly with priming agent and its osmotic potenial. Therefore, the soaking duration is a determining factor in inducing the desired effects of priming (Vanangmudi et al. 2000; Giri & Schillinger, 2003; Afzal, Barsa, et al., 2005; Subedi & Ma, 2005; Farooq, Barsa, Tabassum, et al., 2006; Atrip & O'Reilly, 2007; Dezfuli et al., 2008; Govinden-Soulange & Levantard, 2008; Yari et al., 2010).

Yari et al. (2010) studied the effect of priming duration on germination and early growth of two wheat cultivars (Azar-2 and Sardari 101). Seeds were primed for 12 , 24, or 36 h in 10 or 20% PEG, 2 or 4% KCl, or 0.5 or 1% KH_2PO_4. The results showed that the greatest germination percentage was recorded in cv. Azar-2 when the seeds primed with 20% PEG for 12 h and the highest stem length was obtained for seeds primed with 10% PEG for 24 h. Moreover, Yari et al. (2012) tested the effect of soaking three wheat cultivars (Fajer, Sherodi and Taram) in 0.5 or 1% $CaCl_2$ solutions for 12, 24, or 36 h. They concluded that soaking for 24 h was suitable for all three cultivars in terms of increasing the germination percentage. Dezfuli et al. (2008) examined the influence of hydropriming duration on the seed vigor of two maize inbred lines, namely B73 and MO17. Soaking the seeds of both inbred lines for 36 h was the most effective in increasing the germination percentage, germination index, vigor index, and radical and colepotile length, and in decreasing mean germination and $T_{50\%}$. Similarly, Rouhi et al. (2011) soaked the seeds of tall fescue (*Festuca arundinacea*) in distilled water for 12, 14, 36 or 48 h at 15 or 20ºC in the dark and then dried them back to their original weight. The results showed that all treatments significantly increased the germination capacity, germination rate, coleoptile length, radical length, seedling length, and seedling dry weight compared with unprimed seedlings. However, soaking for 12 h at 15ºC was the most effective treatment.

A significant effect of soaking duration on the germination capacity, germination rate and shoot length of tomato seeds primed with PEG 6000 has been observed (Asgharipour et al., 2014). Akter et al. (2018) reported that, although hydropriming maize seeds for 24 or 48 h effectively ameliorated the salt stress compared with unprimed seeds, soaking for 48 h was more effective than 24 h. Similarly, although halopriming with -0.2 MPa NaCl, -0.2 MPa PEG 6000 or hydropriming for 8 or 16 h improved the measured germination indices of sesame seeds under normal and drought stress conditions, osmopriming with PEG for 16 h was the most effective treatments. (Morteza et al., 2017).

It has been reported that the optimum length of soaking barley seeds was between 12 and 16 h (Rashid et al., 2006) and from 6 to 8 h for mungbean (*Vigna radiata*) (Rashid et al., 2004). The safe time limit for soaking rice and maize was 24 h and 10 h for chickpea (Harris et al., 1999). Similarly, the safe limit for pinto bean (*Phaseolus vulgaris*) was reported to be 7 h and longer soaking resulted in negative impact on seed quality as indicated by reduction in grain yield (Ghassemi-Golezani et al., 2010). Similarly, when the seeds of two wheat cultivars were soaked for 12, 24 or 36 h in water, or in 2 or 4% KCl, 0.5 or 1% KH_2PO_4, or 10 or 20% PEG, the safe limit for soaking was less than 12 h as longer soaking tended to decrease the germination percentage and rate (Giri & Schillinger, 2003). Furthermore, the radical length of endive (*Cichorium endivia*) and chicory seedlings raised from primed seeds was lower with 30 min than with 15 min priming (Tzortzakis, 2009). Teshome et al. (2018) also reported that the safe limit of soaking sorghum varieties (Abshir, Dekeba, Meko-1, Melkam and Teshale) in water, 0.2 g l^{-1} $ZnSO_4$ or 9 g l^{-1} urea solutions is 10 h beyond which germination was reduced. This reduction was attributed to ion leakage and/or ion accumulation. Thus, it is essential to determine the maximum length of time for which seeds can be soaked, beyond which damage to seed or the subsequent seedlings occurs. In this regard, Harris et al. (1999), and Harris et al. (2001) suggested the term known as the safe limit of soaking which should be determined for each variety to prevent germination once seeds are removed from the soaking medium.

4- Responsivity of seed species and varities to priming

Variable responses of seeds of plant species and varieties to pre-sowing treatments in many studies have been reported. For instance, a comparative investigation of the influence of pre-sowing seed treatments on a number of crops including tomato, onion and watermelon was conducted by Maiti et al. (2011). The results revealed that although hydropriming, 3% KNO_3 and -1.0 MPa PEG increased the growth and yield of all crops, there was variation in their response to priming treatments. It has also been reported that the response of two wheat cultivars to halopriming with 50 mM of $CaCl_2$, NaCl or $CaSO_2$ was different (Afzal et al., 2008)

Yari et al. (2012) concluded that the responsivity of three wheat seed cultivars namely, Fajer, Sherodi, and Taram to different concentration of $CaCl_2$ was variable. Variation in responsivity of number of wheat cultivars to priming treatments has been reported by Afzal, Barsa, Hameed, et al. (2006); Afzal et al. (2008), Yari et al. (2010), Nawaz et al. (2012), and Yari et al. (2012). Moreover, Dazfuli et al. (2008) also concluded that the response of two maize cultivars (B73 and MO17) to hydropriming, osmopriming, and PEG-6000 was different. Variable response between two rice cultivars to nitrophos as a priming media was also reported by Farooq, Barsa, Hafeez, et al. (2005). Similar results were reported by Sliwinska and Babinska (1999) with two cultivars of beetroot.

In addition, Podlaski et al. (2003) observed that the responses of two varieties of parsley to priming were different. A similar result was reported by Jisha and Puthur (2014) with three varieties of green gram . A variable response to halopriming between lemon balm and cumin (*Cuminum cyminum*) was also reported by Younesi and Moradi (2015). Similarly, Ben Fredj et al. (2014) reported that although halopriming with NaCl alleviated the profound effect of salinity on four coriander cultivars, the Tunisian one was more responsive than the other cultivars. It has also been found that halopriming with 100 mM NaCl of three sugarcane cultivars varying in their salt tolerance resulted in significant improvement in seed germination and germination rate of the tolerant and moderately tolerant varieties compared with the sensitive one under saline conditions (Patade et al. 2009).

Halmer (2004) claimed that, in general, low vigour seeds may benefit more than high vigour seeds from pre-sowing seed treatments. Similarly, Afzal et al. (2004) have also claimed that the performance of low vigour seeds can be enhanced by seed priming. Consistently, it has been reported that halopriming low quality cv. Mission muskmelon seeds, artificially aged for 20 or 40 h, with KNO_3 remarkably enhanced both the germination capacity and germination rate at 17˚C compared with unprimed seeds. The final germination of primed seeds was 95 and 97% for 20 and 40 h aged seeds, respectively, compared with 30 and 0% recorded in untreated seeds. Furthermore, while hydropriming resulted in the enhancement of storability of low vigour seeds of cauliflower , it decreased it for high quality seed (Powell et al. 2000).

Conclusion

Rapid and uniform germination or emergence are manifestations of seed vigor, which is a key for plant success in a wide range of environmental conditions. These desired features can be enhanced by seed priming. The beneficial effect of priming is demonstrated by many characteristics, including increased germinability, germination rate, synchronicity, seedling growth and vigor, early maturity, salt and drought tolerance and disease resistance. However, many priming agents can be used and each potential treatment may induce desired or undesired consequences. Seed species or varieties, the composition and concentration of the priming medium, and duration of soaking in the priming solution are all factors influencing the successes of priming. Accordingly, there is no particular standard priming regime that can be recommended for use with all seed species, varieties and cultivars. In principle, seed priming offers a safe, inexpensive and technologically simple opportunity to significantly improve crop performance. Where seeds are primed on a large scale by commercial or centralised seed suppliers before distribution, it may be realistic to expect these organisations to test the optimum priming regime for different seed batches along with viability and vigour tests that are already routine. On the other hand where seed priming is intended to be an on-farm technique for farmers to use with seeds they purchase or have saved from year to year, the focus of research should be on selecting priming protocols that have both wide application and wide safety margins, as well as simple methodology and low cost.

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