Osmopriming with Polyethylene Glycol (PEG) for Abiotic Stress Tolerance in Germinating Crop Seeds: A Review

Chu Lei 1, Muthukumar Bagavathiannan 2, Huiyong Wang 1, Shaun M. Sharpe 3, Wenting Meng 1 and Jialin Yu 2,*

1 Co-Innovation Center for Sustainable Forestry in Southern China, College of Forestry, Nanjing Forestry University, Nanjing 210037, China; chuleinjfu@njfu.edu.cn (C.L.); Wanghuiyong@njfu.edu.cn (H.W.); eng7220@outlook.com (W.M.)
2 Department of Soil and Crop Sciences, Texas A&M University, College Station, TX 77843, USA; muthu.bagavathiannan@tamu.edu
3 Saskatoon Research and Development Centre, Science and Technology Branch, Agriculture and Agri-Food Canada/Government of Canada, Saskatoon, SK S7N 0X2, Canada; shaun.sharpe@canada.ca
* Correspondence: yu.jalilin@tamu.edu; Tel.: +1-979-470-7647

Abstract: Abiotic stresses such as drought, extreme temperature, and salinity can negatively impact seed germination and plant growth and have become major limitations to crop production. Most crops are vulnerable to abiotic stress factors during their early growth phase, especially during seed germination and seedling emergence. Rapid crop seed germination and seedling establishment is known to provide competitive advantages over weeds and improve yields. Seed osmopriming is defined as a pre-sowing treatment in which seeds are soaked in osmotic solutions to undergo the first stage of germination, but radicle protrusion has not occurred. The process of osmopriming involves prior exposure of seeds in low-water-potential solutions. Osmopriming can generate a series of pre-germination metabolic activities, increase the antioxidant system activities, and prepare the seed for radicle protrusion. Polyethylene glycol (PEG) is a popular osmopriming agent that can alleviate the negative impacts of abiotic stresses. This review summarizes research findings on crop responses to seed priming with PEG under abiotic stresses. The challenges, limitations, and opportunities of using PEG for crop seed priming are discussed with the goal of providing insights into future research towards effective application of seed priming in crop production.

Keywords: abiotic stress; drought stress; temperature stress; salinity stress; seed germination; seed priming

1. Introduction

Abiotic stresses are a common cause of crop yield reduction worldwide. Yield loss may occur when crops suffer from various abiotic stresses such as cold, heat, drought, freezing, flooding, heavy metals, UV-light, and mineral deficiency [1–6]. Abiotic stresses may occur individually, sequentially, or concurrently. However, plants may suffer greater detrimental effects when they are exposed to multiple abiotic stresses, such as cold and drought, heat, and heavy metal, as well as drought and heat, than when they are exposed to each individual stress [7–10].

In recent years, a growing amount of research has been conducted to investigate the impact of multiple stress factors on crop growth and productivity [7,11–14]. Various techniques such as proper agronomic practices (e.g., pest management, soil fertility management, and seed priming), traditional breeding, and modern biotechnology have been employed to enhance crop tolerance to abiotic stresses [15–17]. Traditional breeding methods such as hybridization and selection, as well as mutation breeding, have contributed considerably to the generation of stress-tolerant crops [16,18–22]; however, the process is fairly time-consuming. The ‘omic’ biotechnologies (e.g., transcriptomics, proteomics, and genomics) can be used to identify the genes that are associated with stress tolerance in crops.
The identified genes can be directly introduced into the elite crop varieties or silenced to make a transgenic plant, which is less time-consuming than traditional breeding [16,23–25]. Transgenic crops with improved stress tolerance have been successfully developed and cultivated in field conditions [26]. Nevertheless, transgenic technologies are not readily accepted in many countries [27,28].

Agronomic management approaches such as appropriate fertilization, irrigation, exogenous application of biostimulants, and/or selection of crop varieties have been shown to be valuable in mitigating the adverse effects of abiotic stresses [16,29,30]. Among these management approaches, seed priming is a common tactic to protect various vegetable and row crops against unfavorable environmental stresses without considerably affecting crop fitness and productivity [4,31–33]. Primed seeds generally show an improved germination rate, uniform germination, and early emergence [5,17,34,35]. During priming, seeds are hydrated in low water potential solutions to initiate germination, but radical protrusion through the testa has not yet happened [34,36]. When seeds are primed, the water supply is controlled at a level below that needed to complete seed germination, but is enough to activate a series of metabolic physiological reactions related to the initial germination [4,34,35,37–41].

Osmopriming is a commonly adopted priming technique and offers a highly attractive solution for improving seed germination performance and crop stand establishment [34,35]. A variety of chemicals, such as CaCl$_2$, KNO$_3$, KCl, K$_3$PO$_4$, NaCl, PEG, and mannitol, have been examined as potential osmopriming agents [5,35]. Among these, PEG is the most commonly used priming osmoticum. PEG is chemically inert and does not impose damaging effects on seed embryos [42]. In addition, PEG is non-damaging to proteins and does not penetrate seed tissues due to its large molecular size [42–46].

In most cases, PEG-primed plants exhibit positive effects on seed germination, seedling establishment, and yield, but the benefit is variable depending on several factors such as crop species and stress type [47–50]. Previous reviews on this topic have mainly focused on seed priming with various agents [4,35,51], but priming with PEG against abiotic stresses has not been well analyzed. Here, we review PEG-primed crop tolerance to drought, suboptimal temperature, salinity, or combined stresses. The effectiveness of PEG priming to improve seed germination and seedling establishment under adverse environmental conditions, and associated mechanisms are discussed by stress type with the aim of utilizing PEG priming in minimizing adverse environmental impacts on crop production and providing insights for future research.

2. Consequences of Abiotic Stresses and Their Mitigation through PEG

2.1. Drought Stress

Drought stress is a common abiotic stress affecting crop productivity [1,52]. Oxidative stress accompanies almost all abiotic stresses and occurs as a result of reactive oxygen species (ROS) in plants [53]. Under adverse conditions, plants increase the production of ROS including hydrogen peroxide (H$_2$O$_2$), hydroxyl radicals (·OH), superoxide radicals (O$_2^-$), and singlet oxygen (·O$_2$) [5,54,55]. These ROS interact with cellular constituents, leading to a series of oxidative damages on carbohydrates, chlorophyll, lipids, DNA, and protein [1,54,55]. Water deficit also causes other damaging effects on plant growth including epinasty, stomatal closure, and decreased photosynthesis [1,5,56].

As shown in Table 1, drought stress considerably decreased the germination performance of asparagus (Asparagus officinalis L.) [32], barley (Hordeum vulgare L.) [31], celery (Apium graveolens L.) [57], cumin (Cuminum cyminum L.), rice (Oryza sativa L.) [58,59], sorghum (Sorghum bicolor L. Moench) [5], and wheat (Triticum aestivum L.) [2]. However, under the conditions of drought stress, the above-mentioned crops pretreated with PEG have shown improved seed germination and seedling establishment [31,57,60–64].

In response to abiotic stress, plants utilize a complex antioxidant defense machinery that protects them against the damaging effect caused by oxidative stress [5,7,53]. The capacity of the antioxidant defense system comprises enzymatic and non-enzymatic an-
The main free radical scavenger of enzymatic antioxidants includes ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR), guaiacol peroxidase, glutathione reductase (GR), glutathione-S-transferase, glutathione peroxidase (GPX), monodehydroascorbate reductase, and superoxide dismutase (SOD), while the main non-enzymatic antioxidants include ascorbic acid (vitamin C), carotenoids, glutathione, and tocopherols (vitamin E) [53,65,66].

PEG priming caused a rapid enhancement of some antioxidant enzymes in seedlings exposed to drought stress, thus mitigating the detrimental effect on seed germination and stand establishment [5,58,67]. For example, PEG-primed rice exhibited higher seed germination and seedling growth rates with higher GPX activity compared to unprimed plants [58]. PEG-primed rice seedlings exhibited elevated levels of MnSOD in drought conditions [58]. Zhang et al. [67] reported that PEG-primed perilla mint (Perilla frutescens L. Britt) increased protective enzyme activities of CAT, peroxidase (POD), and SOD in plant leaves. In other research, Zhang et al. [5] found that unprimed sorghum seedlings demonstrated increased electrolyte leakage and O$_2^-$ content, and decreased membrane stability under drought conditions; PEG-primed sorghum seedlings exhibited less lipid peroxidation, improved cell membrane stability, and enhanced activities of APX, CAT, POD, and SOD. Overall, previous evidences collectively indicate that enhanced drought tolerance in PEG-primed plants is likely due to elevated antioxidant activities that restricted the accumulation of ROS [5,9,53,65–67].

2.2. Temperature Stress

Plants display optimal germination and emergence at an ideal range of temperature to which they have adapted [68–72]. In contrast, under unfavorable temperature conditions, seed germination and seedling establishment are negatively affected [70,73,74]. Temperature stress can be classified into low positive temperature stress (chilling), negative temperature stress (frost), or high temperature stress (heat) [70]. A great amount of research has been performed with the objective of improving crop performance under suboptimal temperature conditions [68,69,71,72]. However, temperature stress is still one of the major abiotic factors limiting crop productivity.

Seed priming with PEG resulted in earlier and synchronized seed germination in various crops such as alfalfa, cereal, turfgrasses, and vegetable crops upon exposure to low or high temperature stress (Table 1) [33,57,62,64,75–80]. For instance, seed priming with PEG effectively promoted seed germination and seedling establishment of soybean [Glycine max (L.) Merr.] [81] and masson pine (Pinus massoniana L.) [82] under negative temperature stress, as well as carrot [78] and leek [80] under high temperature stress. Priming benefits are more pronounced under temperature stress than in optimal temperature conditions [35,51,83]. For instance, Patané et al. [83] reported that the beneficial effect of PEG priming in sweet corn was only evident when plants were exposed to the suboptimal temperatures rather than optimal conditions.

Priming with PEG rapidly enhanced α-amylase activity and increased fructose and glucose content in rice [75]. Plants primed with PEG exhibited improved α-amylase and/or β-amylase activities, which facilitated starch degradation and sugar accumulation, leading to a greater respiration rate, seed viability, seed germination rate, and seedling establishment than unprimed plants [9,12,72,84–88]. Nevertheless, excessive priming, even in an optimal PEG solution, may disrupt α-amylase activity, and thus lower seed germination rate and cause abnormal plumule and radicle growth [89,90]. It has been suggested that appropriate priming regimes including priming solution concentration, priming duration, and priming temperature can all influence the effectiveness of seed priming [4,51,91–94].

Seed priming with PEG at low temperature conditions facilitated the differentiation and duplication of mitochondria [95]. The increased mitochondrial enzyme activity might help improve the enzymatic activities involved in seed reserve mobilization, such as fats, proteins, and sugars [96–98], enhancing the tolerance to chilling injury [99]. Priming with
PEG also enhanced the enzymatic activities of acid phosphatase and esterase, as well as RNA synthesis in various crop species such as celery, onion (*Allium cepa* L.), lettuce, soybean, and sweet corn (*Zea mays* L.) [100].

A review of current literature indicates that antioxidant machinery has not been extensively studied for PEG-primed plants under the condition of temperature stress. Bailly et al. [101] noted that CAT played an important role in promoting sunflower (*Helianthus annuus* L.) seed germination after priming with PEG. Recent evidences indicated that other osmotica can significantly enhance the enzymatic activity in plants growing under low temperature stresses [99,102–105]. For instance, Guan et al. (2009) noted that seed priming with chitosan enhanced CAT and POD activities, along with faster germination rate, increased shoot and root length, and overall plant biomass in two corn cultivars with distinct chilling stress tolerance. Kaur and Goyal [104] recently reported that antioxidants play a key role in improving tolerance of Egyptian clover (*Trifolium alexandrinum* L.) to low temperature stress after priming with salicylic acid.

Although PEG-primed plants exhibited superior tolerance to abiotic stresses in a wide range of crop species [4,35], the use of PEG as an osmotica is not recommended for the seeds of high-tannin sorghum cultivars [106]. Tannins in the seed coat are desirable and protect seeds from weathering and reduce the vulnerability of seeds to birds, insects, and mold attacks [107]. High tannin content may also help improve seedling emergence under suboptimal temperature conditions [107]. However, tannins exhibit higher binding affinity with PEG (Silanikove et al., 1996). Patanè et al. [106] reported that after priming with PEG, tannin content consistently reduced in the seeds of high-tannin cultivar of sorghum [106,108], thus reducing the beneficial effect of seed priming. In order to preserve the benefits of seed priming, Patanè et al. [106] recommended the use of other osmotica (instead of PEG) or the adoption of biological agents for priming high-tannin sorghum cultivars.

### 2.3. Salinity Stress

Soil salinity is a serious problem limiting crop production. Salinity stress is especially problematic in arid and semi-arid regions of the world [13]. Salinity stress reduces soil water availability for plant roots by lowering osmotic potential [109]. The germination of most crops fails under severe or even moderate salinity stress [34,110,111]. Salinity negatively influences seed germination through ionic imbalances, osmotic stress, or mixed effects of these factors, causing detrimental impacts on enzymes, proteins, cell organelles, plasma membranes, thereby reducing respiration and photosynthetic rates [13,112]. In addition, salinity stress changes the signal balance in higher plants. Increasing salinity stress is linked with increases in abscisic acid and jasmonates as well as reductions in auxin, cytokinin, gibberellins [13,113]. Salinity stress can significantly delay seed germination and reduce the percentage of seeds that are capable of germinating [13]. Plants generally exhibit a decrease in biomass accumulation upon exposure to salinity stress [36].

The effectiveness of seed priming with inorganic salt, such as CaCl₂, KCl, KNO₃, and MgSO₄, for overcoming salinity stress has been noted in a variety of crop species (Table 1) [4,114–117]. Shahi-Gharahlar et al. [117] reported that priming with PEG was less effective for decreasing salinity damage than with NaCl in summer squash (*Cucurbita pepo* L.) [117]. Nevertheless, extensive studies revealed that PEG priming is a successful approach to improve germination performance in various plant species including amaranth (*Amaranthus* spp.) [118], pepper (*Capsicum annuum* L.) [119], tomato (*Solanum lycopersicum* L.) [120], sugarcane (*Saccharum officinarum* L.) [121], soybean [122], wheat [123], and sweet corn [83] under salinity stress.

Salt tolerance conferred by seed priming is linked to an enhanced ability for osmotic adjustment as primed plants exhibited elevated concentrations of Ca²⁺, K⁺, and Mg²⁺ ions and reduced concentrations of Cl⁻ or Na⁺ ions in roots and a greater amount of soluble sugars and organic acids in leaves compared to the unprimed plants [4,34,35]. Priming of wheat seeds with choline enhanced salinity tolerance by reducing the toxic elements of Na⁺ and Cl⁻, and by increasing the beneficial elements of Ca²⁺ and K⁺ [124]. Priming
with melatonin enhanced indole-3-acetic acid, total phenolic content, as well as Ca\(^{2+}\) and K\(^{+}\) in the leaves of faba bean (*Vicia faba* L.) under salinity stress [125]. However, these physiological parameters have not been studied in PEG-primed plants under salinity stress, and therefore further research is needed to understand the specific mechanisms of PEG priming in protecting plants against salinity stress.

### 2.4. Multiple Abiotic Stresses

The concurrent occurrence of multiple abiotic stresses may result in additive or synergistic effects on plant growth. Consequently, combined occurrence of multiple abiotic stresses can be more damaging than when they occur sequentially or individually [4, 68]. Under natural conditions, multiple abiotic stresses may commonly occur [55]. However, most PEG priming studies reported to date were conducted under the conditions of a single abiotic stress [5, 33, 64, 75, 80, 83, 126–128].

As shown in Table 1, a limited number of studies have investigated the effectiveness of PEG priming against multiple abiotic stresses and shown promising results [32, 126–129–132]. Priming with PEG effectively enhanced seed germination and early seedling establishment in asparagus and spinach (*Spinacia oleracea* L.), especially when exposed to combined drought and low temperature stresses [32, 129, 130, 132, 133]. Seed priming with PEG also enhanced tolerance to simultaneously occurring drought and salinity stresses in sunflower [131]. However, the specific mechanisms of improved seed germination and emergence for PEG priming under multiple abiotic stresses, particularly at the cellular and molecular levels, have not yet been elucidated.

### Table 1. A summary of published reports on the effectiveness of PEG priming plants for abiotic stress tolerance in crops.

| Abiotic Stress Type | Crop Species                  | Brief Summary                                                                 |
|---------------------|-------------------------------|-------------------------------------------------------------------------------|
| Drought stress      | Asparagus                     | Priming with PEG resulted in early seed germination and seedling emergence, as well as superior seedling vigor [32]. |
|                     | Barley                        | Priming with PEG improved seed germination rate, root and shoot length, and seedling biomass [31]. |
|                     | Sorghum                       | Priming with PEG enhanced seed germination and seedling emergence. It also increased the antioxidant activities of APX, CAT, POD, and SOD, and improved the levels of several compatible solutes including free amino acid, proline, reducing sugar, soluble sugar, and soluble protein [5]. |
|                     | Cumin                         | Priming with PEG accelerated seed germination and seedling stand uniformity [132]. |
|                     | Rice                          | Priming with PEG improved seed germination and emergence rates, plumule height, and radicle length [89]. |
|                     | Rice                          | PEG priming improved seed germination and seedling growth rate. In addition, PEG-primed plants had increased GPX activity and overexpressed MnSOD compared to unprimed plants under drought stress [58]. |
|                     | Rice                          | PEG-primed plants exhibited improved seed vigor, seedling growth, and enhanced tolerance under drought stress [59]. |
|                     | Mountain rye (*Secale montanum* L.) | PEG priming increased seed germination rate, seedling vigor, and seedling length [2]. |
|                     | Wheat                         | PEG priming increased seed germination percentage, germination index, and seedling length. PEG priming also increased APX and CAT activities [60]. |
Table 1. Cont.

| Abiotic Stress Type                  | Crop Species | Brief Summary                                                                                                                                 |
|-------------------------------------|--------------|----------------------------------------------------------------------------------------------------------------------------------------------|
| Temperature stress                  | Asparagus    | Priming with PEG enhanced seed germination, seedling emergence, as well as seedling vigor under temperature stress [32].                     |
|                                     | Alfalfa      | Priming with PEG improved germination speed and germination rate [64].                                                                          |
|                                     | Soybean      | PEG-primed plants exhibited early and synchronous germination at low temperature stress [81].                                                |
|                                     | Lettuce      | Priming with PEG speeded seed germination and resulted in early emergence [61].                                                               |
|                                     | Common carpetgrass (*Axonopus affinis* Chase); Centipedegrass [*Eremochloa ophiuroides* Munro. (Kunz)] | Priming with PEG increased seed germination percentage and resulted in early germination for common carpet grass and centipede grass [33]. |
|                                     | Dusty miller (*Senecio cineraria* DC.) | PEG priming increased the germination percentage and resulted in early seed germination [134].                                             |
|                                     | Leek         | PEG-primed plants had improved germination rate and final percentage of germination at suboptimal temperatures [62].                         |
|                                     | China aster  | Priming with PEG resulted in early germination and increased germination index [126].                                                          |
|                                     | Carrot       | Priming with PEG improved seed germination performance under high temperature stress by increasing ethylene production [78, 79].            |
|                                     | Leek         | Priming with PEG improved seed germination and seedling emergence at high temperature stress [80].                                          |
|                                     | Leek         | Priming with PEG improved seed germination and seedling emergence at high temperature stress [80].                                          |
| Salinity stress                     | Pepper       | PEG-primed plants had improved germination performance and seedling growth under saline soil [119].                                           |
|                                     | Sunflower    | Priming with PEG improved germination performance and seedling vigor under salinity stress [135].                                              |
|                                     | Amaranth     | PEG priming increased seed germination and seedling growth [118].                                                                             |
|                                     | Sugarcane    | PEG-primed plants had improved shoot growth, reduced leaf senescence, and exhibited better osmotic adjustment through accumulation of glycine betaine and dissolved ionic solutes [121]. |
|                                     | Sweet sorghum| The beneficial effects of PEG priming are evident under suboptimal temperatures rather than the optimal temperature [83].                   |
|                                     | Tomato       | PEG priming increased seed germination percentage, seedling vigor, and biomass [120].                                                          |
|                                     | Wheat        | PEG-primed wheat seeds showed improved germination and seedling emergence compared to non-primed seeds [123].                                 |
| Drought + low temperature stress    | Asparagus    | PEG priming resulted in early seed germination and seedling emergence under drought and low temperature stresses [32].                       |
| Drought + low temperature stress    | Spinach      | PEG-primed plants exhibited improved seed germination percentage and seedling uniformity under drought and low temperature stresses [129].       |
| Drought + salt                      | Sunflower    | PEG priming increased seed germination percentage, germination rate, root and shoot length, seedling weight and vigor [131].                  |

Abbreviations: APX, ascorbate peroxidase; CAT, catalase; GPX, glutathione peroxidase; PEG, polyethylene glycol; POD, peroxidase; SOD, superoxide dismutase.

3. Conclusions

The effectiveness of PEG priming against different abiotic stresses has been shown in a wide range of crop species. PEG primed seeds generally resulted in earlier and synchronized seed germination largely due to enzyme activation, increased germination-promoting metabolites, and osmotic adjustment. The reported mechanisms of PEG priming against drought, temperature, or salinity stress are summarized in Figure 1. However, only a very few studies have examined the effects PEG priming against combined abiotic stresses. The specific mechanisms of PEG priming against abiotic stresses, especially under the conditions of multiple stresses, are not yet fully understood and our knowledge of the cellular and molecular levels changes following plant seeds after seed priming remains limited. Future research in this report is expected to facilitate broader adoption of this technology.
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