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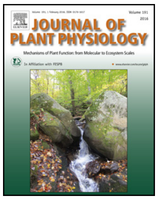

Physiology

Molecular processes induced in primed seeds—increasing the potential to stabilize crop yields under drought conditions☆

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ABSTRACT

Environmental stress factors such as drought, salinity, temperature extremes and rising CO_2 negatively affect crop growth and productivity. Faced with the scarcity of water resources, drought is the most critical threat to world food security. This is particularly important in the context of climate change and an increasing world population. Seed priming is a very promising strategy in modern crop production management. Although it has been known for several years that seed priming can enhance seed quality and the effectiveness of stress responses of germinating seeds and seedlings, the molecular mechanisms involved in the acquisition of stress tolerance by primed seeds in the germination process and subsequent plant growth remain poorly understood. This review provides an overview of the metabolic changes modulated by priming, such as the activation of DNA repair and the antioxidant system, accumulation of aquaporins and late embryogenesis abundant proteins that contribute to enhanced drought stress tolerance. Moreover, the phenomenon of "priming memory," which is established during priming and can be recruited later when seeds or plants are exposed to stress, is highlighted.

1. Introduction

Monitoring of global climate changes in recent decades has indicated a disturbing trend of intensification of extreme weather events, including the appearance of more frequent and more intense periods of drought. More than 20% of cultivated land worldwide is affected by salt stress due to the increasing use of poor quality water for irrigation and soil salinization (Gupta and Huang, 2014). Climate warming and the observed increase in atmospheric greenhouse gases concentration, particularly CO_2, are unequivocal (IPCC, 2014). While plants may benefit from elevated CO_2, they could suffer from drought and heat stress (Qaderi et al., 2006). The projections of future climate change and the resulting risks and impacts on global agriculture predict negative impacts on average crop yields and increases in yield variability (IPCC, 2014). Since the 1960s, a gradual expansion of the drought in areas of cultivation has been observed, which together with an increased intensity and frequency of drought leads to a significant decline in global agricultural production (Li et al., 2009). It is believed that, on a global scale, among all abiotic stressors, drought is the main factor limiting both growth and productivity of plants (Bohnert et al., 1995).

Drought stress is defined as a disorder of intracellular equilibrium in water relations that is the result of predominance in loss of water through transpiration over the absorption of new water by plants (Farooq et al., 2009a). Water stress leads to a series of adverse changes in physiological and biochemical processes in plant cells. Water deficiency results in growth retardation, reduction in photosynthetic efficiency, disorder of ion homeostasis, and contributes to a significant increase in the level of reactive oxygen species (ROS), causing oxidative damage to cellular components (Farooq et al., 2012).

As drought stress is the most severe factor limiting crop productivity and a major threat of famine in many regions of the world, all studies leading to increased drought stress tolerance by plants, mainly crops, should receive much attention. It appears to be important to increase our basic knowledge of water stress tolerance in cultivated plants and find effective methods to mitigate the adverse effects of drought on plants (Fleta-Soriano and Munné-Bosch, 2016). Currently, increased resistance to drought stress can be achieved by several different strategies (Shanker et al., 2014). The most cost-effective approach seems to be the use of appropriate factors at various stages of plant development.

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Methods developing in the direction of imparting higher drought tolerance on plants include: supplying plants with silicon, exogenous application of growth regulators or osmoprotectants and seed priming (Farooq et al., 2009a). Such techniques are particularly promising in countries where cultivation of GMOs is highly restricted.

2. An overview of priming techniques: methods and agents

Seed priming is a pre-sowing treatment that involves a control hydration of seeds that permits pre-germinative metabolic events to proceed while preventing radicle protrusion. Radicle protrusion is considered the completion of germination (Bewley et al., 2013). A common feature of all priming techniques that distinguishes them from other pre-sowing treatments is the partial hydration of seed. Currently available priming methods vary in the technique of water application and include: hydropriming (seeds are soaked in predetermined amount of water or imbibition periods are limited), osmopriming (seeds are soaked in osmotic solutions e.g., polyethylene glycol, mannitol, sorbitol, glycerol or in salt solutions), matrix priming (seeds are mixed with organic or inorganic solid materials and water in known proportion) and drum-priming (seeds are rotated in drum and water is added gradually as water vapour) (Jisha et al., 2013; Paparella et al., 2015). In all of these treatments, the completion of radicle emergence is prevented by a restricted amount of water provided to the seed (hydropriming, solid matrix priming, drum-priming) or decreased water potential (Ψ) of the imbibition medium by the use of osmotic solutes (osmopriming) (Bewley et al., 2013). Primed seeds can be dried back to their original moisture content, which allows convenient storage of such seeds and subsequent distribution to the grower.

Hydropriming, osmopriming or drum-priming can be used as successful delivery mechanisms of additional chemical substances, i.e. plant growth regulators, stimulators or biologically active compounds. This approach includes a wide range of both natural and synthetic compounds such as antioxidants (ascorbic acid, glutathione, tocopherol, melatonin, proline), hydrogen peroxide, sodium nitroprusside, selenium, fungicide etc. (Di Girolamo and Barbanti, 2012; Jisha et al., 2013; Paparella et al., 2015). Several studies have indicated a positive impact of priming with various priming agents under a wide range of environmental conditions (Duan et al., 2007; Guan et al., 2009; Anosheh et al., 2011; Patade et al., 2012; Khaliq et al., 2015). The use of priming with beneficial microorganisms is becoming an integral component of agricultural practice (Glick, 2012; Timmusk et al., 2014). The effectiveness of seed priming depends on the choice of appropriate conditions according to plant species, to cultivars within a species and even to seed lots within the same cultivars. The major factors affecting the efficiency of the priming include: light, temperature, aeration of osmotic solution, duration of the priming process and post-hydration drying (de Lespinay, 2009). Indeed, priming techniques used in agriculture differ with effectiveness, economic profitability and plant species susceptibility. Moreover, primed seed storage is a major challenge involved in seed priming (Hussain et al., 2015).

2.1. The agricultural relevance of priming

In agriculture, from an economic point of view, the quality of dry seeds is of particular importance. Seeds are starting material for crop production and crucial for achieving a good harvest. Agricultural performance is influenced by several parameters of seed quality such as total emergence, the rate and uniformity of emergence, emergence under suboptimal conditions and seed longevity.

Seed germination is a crucial phase in the plant life cycle, and is strictly regulated by endogenous and exogenous factors, including environmental ones, mainly water availability, as water relations of the seed and of the soil, and temperature (Bewley et al., 2013). Compared with the mature plants, germinating seeds and seedlings are usually more susceptible to abiotic stresses (Li et al., 2013). A sufficient amount of water is indispensable during the germination process, while limitation of water is one of the main causes of the reduction of germination efficiency. Water deficit during imbibition causes not only a delay in emergence, but even inhibition of germination (Farooq et al., 2013). Drought is also responsible for poor seedling establishment (Harris et al., 2002). In mung bean (*Vigna radiata*) drought caused inhibition of seedling growth and the reduction of the percentage of germinated seeds (Sanadhya et al., 2012). The percentage of germinated seeds, radicle and hypocotyl length, and seedling fresh weight of swallow wort (*Cynanchum acutum*) decreased sharply with increasing NaCl concentration and linearly with intensification of drought stress. However, swallow wort seeds were able to germinate at a wide range of salinity and water potentials, which has implications for weed management. (Golzardi et al., 2012).

Priming treatments are used to synchronize the germination of individual seeds. Since certain germination-related processes are initiated, priming generally causes faster germination and emergence, especially under adverse conditions. The priming technique is routinely used in the vegetable and flower seed industries. Some of the priming procedures used in the market are patented and are commercially available (Paparella et al., 2015).

The positive effect of priming on seeds is checked mainly by a germination test under control and stressed conditions. As seed priming is a pre-sowing procedure that has beneficial effects on germination performance, determining future growth and development, it is commonly believed that seed priming affects not only germination, but also successful crop establishment, and priming effects could be passed on to the next generations. In some cases, the effects of seed priming are stronger in more advanced growth stages as shown with tomato (*Lycopersicon esculentum*) (Cayuela et al., 1996). Applying beneficial microorganisms to the seed during priming may further improve establishment of the crop, particularly if seed-applied microorganisms subsequently become established in the root zone of the plant and contribute to longer-term plant health or plant growth promotion (Bennett and Whipps, 2008). The studies of Kaur et al. (2005) have shown that priming can influence seed filling and increase the yield of crops raised from primed seeds. On-farm seed priming with water is a low-cost, low-risk technology that was found to increase the yield of tropical and subtropical annual crops in marginal areas by a combination of better crop establishment and improved individual plant performance (Harris et al., 2005). Moreover, literature data on seed priming have indicated long-lasting effects on plants after germination. For example, wheat (*Triticum aestivum*) seeds soaking in saline solution have been shown to prime plants germinating from the treated seeds so that they are more resistant to salt stress for the whole growing season (Iqbal and Ashraf, 2007). Some stress imprint effects in plants have even been shown to be perpetuated to the next generation (Bruce et al., 2007; Slaughter et al., 2012).

In addition to the increase in the quality of seeds, the priming process improves the tolerance of seeds and seedlings to stress conditions (Jisha et al., 2013; Kubala et al., 2015b). However, the cellular mechanism of seed priming as it relates to improved germination as well as stress-tolerance is not fully understood (Chen and Arora, 2013).

2.2. Mechanisms involved in increased drought stress tolerance

During seed priming, numerous physiological, biochemical and molecular mechanisms are stimulated, which may contribute to improved stress tolerance in plants grown from primed seeds. Most