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Review

Chemical Priming of Plants Against Multiple Abiotic Stresses: Mission Possible?

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Crop plants are subjected to multiple abiotic stresses during their lifespan that greatly reduce productivity and threaten global food security. Recent research suggests that plants can be primed by chemical compounds to better tolerate different abiotic stresses. Chemical priming is a promising field in plant stress physiology and crop stress management. We review here promising chemical agents such as sodium nitroprusside, hydrogen peroxide, sodium hydrosulfide, melatonin, and polyamines that can potentially confer enhanced tolerance when plants are exposed to multiple abiotic stresses. The challenges and opportunities of chemical priming are addressed, with the aim to boost future research towards effective application in crop stress management.

Trends

Plant priming using chemical agents such as sodium nitroprusside, hydrogen peroxide, sodium hydrosulfide, melatonin, and polyamines enhances plant tolerance to different abiotic stresses, improving cellular homeostasis and plant growth under stress conditions.

Commonly employed chemical priming agents share components in their modes of action.

When used against different abiotic stresses, the modes of action of a chemical agent show similarities but also distinct specificities.

Chemical priming through using selected chemical agents is a promising tool against various individual or combined abiotic stresses.

The efficiency of chemical priming depends highly on the mode of application.

Exploring and Exploiting a Physiological Phenomenon

Abiotic stresses such as salinity, drought, flooding, heat, cold, freezing, excess light, UV radiation, and heavy metal toxicity have a significant impact on plant growth and crop yield worldwide. Anthropogenic contributions due to industrialization and urbanization [1] and climate change [2] continue to exacerbate the detrimental effects of these stresses on crop yield, thereby threatening global food security [3]. Plants grown under field conditions may well be exposed during their lifespan to a range of different abiotic stresses that occur sequentially or simultaneously. A combination of different abiotic stresses may act synergistically or additively in terms of impact on plant growth. Stress phenomena that occur simultaneously, such as salinity and heat [4], drought and heat [5], and heavy metals and heat [6], have been shown to be more detrimental to plant growth than each of these stresses individually. Consequently, considerable attention is now directed towards enhancing plant tolerance to multiple biotic stresses [7].

Different methodologies have been employed aiming at enhancing multiple stress tolerance; some are particularly time-consuming (e.g., conventional breeding) and others are currently unacceptable in many countries around the world (e.g., plant genetic modification). As an alternative, plants can be 'prepared' to more successfully tolerate future biotic and abiotic stress conditions through priming. Plant priming (also known as sensitization or **hardening**; see Glossary) can be initiated naturally in response to an environmental stress event that acts as a cue indicating an increased probability of facing that specific stress factor in the future [8]. Following perception of the cue, plants enter the **primed state** (PS) in which activation of protection responses is faster, stronger, or both when a stress pressure is encountered [9–11]. Compared with non-primed plants, the diminished impact of stress exposure on the physiology and growth of primed plants can be remarkable (Figure 1A). Interestingly, plants can also enter the PS by chemical priming, which involves exposure to a priming agent such as a natural or

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synthetic chemical compound. Chemical priming presents opportunities for more effective use of plant priming in plant stress physiology studies and crop stress management.

Use of chemical compounds as priming agents has been found to improve plant tolerance significantly in various crop and non-crop species against a range of different individually applied abiotic stresses (Table S1 in the supplemental information online). Although few studies have employed chemical agents against combined abiotic stresses, these studies are yielding promising results [12,13]. Previous reviews have mainly focused on priming against biotic stresses [9,14] or on the use of individual chemical agents against different abiotic and/or biotic stresses [15,16]. However, not much attention has been paid yet to the use of chemical priming against different, sole and combined, abiotic stresses and its effective application in crop stress management. We discuss key findings from the latest research on chemical priming agents that suggest they could be used to reduce the effects of abiotic stresses in commercial crops. The ability of these agents to enhance tolerance to different abiotic stresses, and the specific aspects of their mode of action summarized in this review, suggest great potential for their use against multiple abiotic stresses. We conclude that further research towards fully elucidating their mode of action would be of great significance for plant stress physiology research. In addition, focusing on specific challenges and opportunities related to this technology, such as the mode of application, new methodologies (e.g., seed priming), and the potential impacts of chemical priming on the environment, would result in the optimum and rapid establishment of this technology in crop stress management.

Promising Chemicals for Enhancing Multi-Stress Tolerance

Many types of molecules have the potential to act under specific conditions as a priming agent against a range of different abiotic stresses [14]. A review of the relevant literature reveals a vast range, including amino acids (e.g., proline [17]), hormones (e.g., salicylic acid [18]), **reactive oxygen–nitrogen–sulfur species** (RONSS [19,20]), and even water (i.e., hydropriming [21]). Some of these agents are effective in inducing plant tolerance to various individually applied abiotic stresses (Table S1).

RONSS

Reactive species have long attracted attention in plant science on the basis of both their protective as well as damaging effects. The priming effect of these molecules is exerted largely through their cellular signaling function, which has been linked to the regulation of transcriptional as well as post-translational phenomena. A multitude of reports demonstrate the priming effect against various abiotic stress factors of reactive oxygen species (ROS), particularly hydrogen peroxide (H_2O_2), when applied in low concentrations. Similar observations have been made for reactive nitrogen species (RNS), nitric oxide (NO) being the most commonly studied representative of this group of compounds. NO is donated indirectly by chemical donors such as **sodium nitroprusside** (SNP). However, most attention is focused on hydrogen sulfide (H_2S), attested by the existence of numerous reports on the potential use of H_2S as a priming agent against virtually any type of abiotic stress [16]. Particularly interesting was the establishment of the existence of a complex interaction between ROS and RNS, in which both reactive species are used by plants as signal transduction molecules during basic biological and cellular processes [22]; it has recently been suggested that reactive sulfur species (RSS) may also play a role in this interaction [23]. Interestingly, it should be noted that RNS and RSS applied at low concentrations have shown growth-promoting properties under non-stress conditions [16,24].

Naturally-Occurring Metabolites

Another category of priming agents currently attracting attention comprises naturally occurring metabolites, including vitamins (e.g., ascorbate [25]) and hormones. The priming function of these molecules may be exerted through indirect mechanisms, such as via osmoprotection (e.

Glossary

Hardening: or cold hardening, the process whereby exposure to low but non-lethal temperatures increases plant tolerance (or the capacity to survive) to subsequent low or freezing temperatures that would be fatal without the hardening treatment.

Heat-shock proteins (HSPs): molecular chaperones that play a role in preventing protein aggregation by assisting refolding, import, and translocation, and are involved in signal transduction and transcriptional activation [96].

Melatonin (*N*-acetyl-5-methoxytryptamine; Mel): has many physiological roles in animals and plants. In plants, it acts as a growth regulator, an antioxidant, and has the capacity to fortify plants against abiotic stresses [33].

Polyamines (PAs): nitrogen-containing compounds of low molecular weight. Spermine (Spm), putrescine (Put), and spermidine (Spd) are considered as the most abundant PAs, and these can also be found in plants. They have important roles not only in plant growth and development but also in plant stress responses [97].

Primed state (PS): the state during which the plants can show enhanced tolerance to a biotic or abiotic stress.

Reactive oxygen–nitrogen–sulfur species (RONSS): chemically reactive molecules containing oxygen [e.g., superoxide radicals ($O^{\bullet -}_2$), hydrogen peroxide (H_2O_2)], nitrogen [e.g., nitric oxide (NO)], or sulfur [e.g., hydrogen sulfide (H_2S)]. They are natural byproducts of the normal metabolism of oxygen, nitrogen. and sulfur and have important roles in cell signaling and homeostasis. Under stress, their concentrations increase dramatically, which may result in damage to cell structures and eventually cell death.

Sodium nitroprusside (SNP): an inorganic compound $Na_2[Fe(CN)_5NO]$ that is used as an NO donor (i.e., NO releasing compound) not only for medical uses but also for plant stress physiology research.