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Review Article

Stimulatory effect of hormonal seed priming in plant tolerance to resist abiotic stress

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Abstract

Plants exposing abiotic stresses such as drought, salinity, heat, cold, and heavy metals that induce complex responses ultimately result in reduced growth as well as crop yield. Phytohormones are widely known for their regulatory functions in controlling plant growth and development. They also act as significant chemical messengers, enabling plants to survive when subjected to a variety of stressors. Nowadays various strategies are employed that can withstand these emergences. In recent years, seed priming has been an indispensable method to induce tolerance against various stresses. The seed priming process is a physiological method that involves hydration for enhancement of seed germination, early seedling growth, and yield under stressed and non-stressed conditions. The seedlings emerging from primed seeds showed early and uniform germination. Moreover, the overall growth of plant is enhanced due to the seed-priming treatments with phytohormone which have become a significant strategy for reducing the impacts of abiotic stress. Therefore, this review analyses the potentiality of priming with several phytohormones to mitigate the negative impacts of abiotic stresses, for improving crop productivity.

1. Introduction

There are some of the major kinds of stresses like heat, drought, cold, and salt stress that crops usually face under adverse weather or soil conditions. Disturbance in equilibrium which produces changes in physiological parameters, and due to stress plant's chemical and physiological changes occur is called stress [1]. In most plants, stress causes a variety of biochemical, physiological, and metabolic changes [2], which may result in oxidative stress and affect plant metabolism, performance, and thereby yield [3]. Abiotic stresses are often interrelated, either individually or in combination; they cause morphological, physiological, biochemical, and molecular changes that affect plant growth and development and ultimately yield. In the present era of global climate change, abiotic stresses are becoming more prevalent. The increasing threat of climate change is already having a substantial impact on agricultural production worldwide causing significant unpredictable loss in agriculture [4] and threat to global food security [5].

Plants are subjected to a variety of abiotic stress such as salinity, drought, high temperature, low temperature, etc. which reduces germination rate and seedling growth with significant variations from crop to crop [6]. Salinity has an adverse effect on seed germination and seedling growth of several crops either by creating an osmotic potential in the the rhizosphere of the plant that inhibits the absorption of water or creates toxic effects to the roots and whole crop because of Na^+ and Cl^- [7, 8]. Drought is one of the most important environmental factors limiting plant growth and productivity. With the increase of drought severity, the drought severity increased, the germination rate linearly decreased in unprimed cotton seeds [9]. Low-temperature conditions decreased plant growth rate because of inhibition of photosynthesis and increasing photo-oxidative injury of the photosystems [10]. Photo-oxidative damage caused lipid peroxidation and degradation of chlorophyll and carotene [110]. Plants exert many physiological and biochemical changes under low-temperature conditions that make them survive under these conditions [10]. Heat stress is often defined as the rise in temperature beyond a threshold level for a period of time sufficient to cause irreversible damage to plant growth and development. The extent to which it occurs in specific climatic zones depends on the probability and period of high temperatures occurring during the day and/or the night [11]. Thus, abiotic stress causes many physiological and biochemical changes in the seedlings, which include the generation of reactive oxygen species [ROS], leading to membrane damage and cell leakage and destruction of photosynthetic components [12].

Various methodologies were adapted from time to time to achieve tolerance against stresses. These include conventional breeding methods such as selection and hybridization and modern methods such as mutation breeding, genetic engineering, etc. [12]. Attempts were also made to produce transgenic plants which can withstand various kinds of stresses [12]. But these methods are time-consuming and demand skills and involve legal and ethical issues. The alternative solution would be more acceptable if it is simple, cost-effective, and can be adopted by the farmers without any complication, and at the same time, it should be effective in manifesting the tolerance.

Seed priming is one such farmer's friendly technique recommended by many researchers for better crop stand establishment and growth even under adverse conditions. It is a simple, safe, economic, and effective approach for enhancement of seed germination, early seedling growth and yield under stressed and non-stressed conditions [13]. In plant defence, priming is defined as a physiological process by which a plant prepares to respond to imminent abiotic stress more quickly or aggressively.

The priming process induces the rate of seed germination and is associated with the initiation of germination-related processes [14] and repair processes [15] and increases various free radical-scavenging enzymes, such as catalase, and peroxidase [16]. Several seed priming methods were successfully used in agriculture for seed conditioning to accelerate the germination rate and improve the seedling uniformity [17, 18]. Moreover, seed priming helps many crops to neutralize the adverse effects of abiotic stress [19]. The various approaches of seed priming are hydro priming, osmopriming, chemical priming, hormonal priming, biological priming, redox priming, solid matrix priming, etc. [111]. Among these techniques, seed priming with phytohormones (hormonal priming) has emerged as a promising strategy in modern stress management as it protects plants against various abiotic stresses by increasing the level of antioxidant enzyme activity, decreasing oxidative damage, and enhancing plant growth. Priming for enhanced resistance to abiotic stress is operating via various pathways involved in different metabolic processes. It is known that seed priming can activate these signalling pathways in the early stages of growth and result in faster plant defence responses. Therefore, the purpose of this review is to summarise the understanding of the regulation mechanism against abiotic stresses through hormonal priming to mitigate the losses occurred in crop production in future.

2. Materials and methods

Relevant literature on hormonal Seed Priming was composed for plant growth and yield attributing activities released up to January 2023. The literature has been searched on the hormonal priming activity of the different phytohormones on different crops. The main keywords were: abiotic tolerant, phytohormones, plant growth, priming, yield etc. GoogleScholar®, ResearchGate®, Web of Science®, PubMed, SciFindern and Scopus® were used as electronic search tools for articles with the several definite keywords. We have reviewed only the manuscripts which are relevant to this article.

3. Results and discussion

3.1 Phytohormones

Plant hormones are known as phytohormones or plant growth regulators (PGRs). These are chemical molecules produced by plants and have important roles in regulating plant growth and development (Fig. 1). Phytohormones function as important chemical messengers and modulate many cellular processes in plants and can coordinate different signalling pathways during exposure to abiotic stresses [20, 21]. Auxins (IAAs), cytokinins (CKs), gibberellins [GAs], abscisic acid (ABA), salicylic acid [SA], and ethylene (ET) are well known phytohormones, essential for plant growth and development [22, 23].

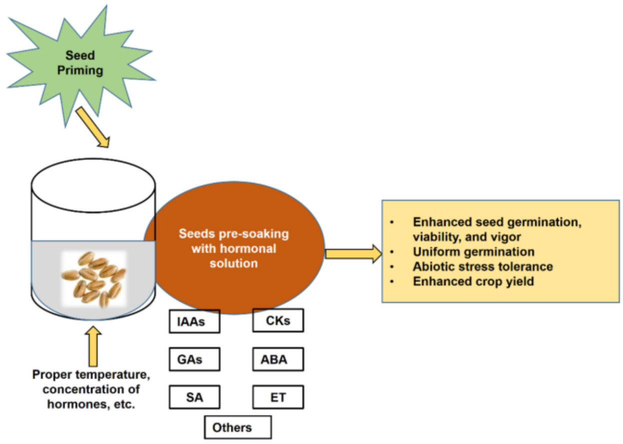

Figure 1. Schematic model showing possible effects of seed priming with phytohormones [24]

3.2 Hormonal priming

Seed priming with hormone solutions is referred to as hormonal priming, and hormonal seed priming plays an important role in seed metabolism [24]. Seeds are pre-soaked with an optimal concentration of phytohormone, which enhances germination, seedling growth and yield by increasing nutrient uptake through enhanced physiological activities and root production [25, 26]. Commonly used plant growth regulators in seed priming are IAAs, CKs, GAs, ABA, SA, and ET.

3.3 Auxins

The role of auxin in plant development is well known; however, its possible function in response to various stresses is poorly understood (Fig. 2). Several studies demonstrate a novel role of auxin signalling and transport in plant tolerance to abiotic stress [27]. Seed priming with IAAs enhances cell division, photosynthetic activities, and translocation of carbohydrates, which results in lateral root initiation, flowering, and good stand establishment [28]. Seed priming with IAAs (1 ppm) enhanced the seedling establishment of *Bouteloua gracilis* [29], and in wheat grass (*Agropyron elongates*), seeds priming with IAAs at 50 ppm improved tolerance to drought stress by enhancing antioxidant enzyme activities such as catalase [CAT], superoxide dismutase [SOD], and peroxidase [30]. Auxin positively modulates root biomass and branching, which might improve water uptake efficiency as well as partly participates in the positive regulation of drought stress resistance through the regulation of root architecture [31]. According to [31], auxin positively regulated the activities of four enzymatic antioxidants (superoxide dismutase, catalase, peroxidase, glutathione reductase) under drought stress conditions, thus conferring effective ROS (reactive oxygen species) detoxification to improve drought stress resistance.

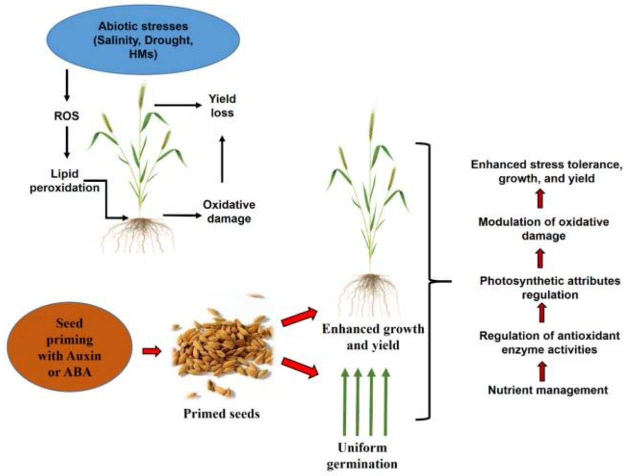

Figure 2. Proposed possible mechanisms used by auxin-and abscisic acid (ABA) priming and their roles on the germination, growth, and development of plants under different stresses [24].

Under salinity stress, wheat seeds priming with IAAs (100, 150 and 200 mg L^{-1}) regulated hormonal homeostasis, which enhanced the CO_2 assimilation rate and ultimately resulted in increased grain yield [32]. SOS pathway (which maintains ion homeostasis under salt stress) modulates root response by regulating PIN2 protein and auxin asymmetric distribution [33]. Also, seed priming with IAAs improved the germination and growth of different species, such as rice (*Oryza sativa*] and pigeon pea (*Cajanus cajan*), under arsenic or cadmium (Cd) stress [34].

High and low day and night temperature (suppose 24-35 °C day temperature and 5-10 °C night temperature) was found to reduce fruit set, pollen grain viability,

Table 1. Seed-priming with cytokinin adopted for developing abiotic stress tolerance in plants.

Plant	Stresses	Responses of Plant	References
Soybean (*Glycine max*)	Drought	Improved drought tolerance in soybean plants	[55]
Pigeon pea (*Cajanus cajan*)	Salt	Prevented the damage caused by the apparatus involved in protein synthesis	[57]
	Cadmium	Tolerance to the effects of Cd stress	[34]
Basil (*Ocimum basilicum*)	Drought	Reduced negative effects of drought stress	[58]
Wheat (*Triticum aestivum*)	Salt	Decreased ABA concentration, increased IAAs concentration, and enhancement of salt tolerance	[59]
	Salt	Improved photosynthetic rate, water use efficiency and stomatal conductance, decreased Na^+ and Cl^- level, increased K^+ level	[60]
	Salt	Decreased electrolyte leakage and conferred salt tolerance	[61]
	Salt	Increased tissue N content and nitrate reductase activity	[62]
	Salt	Induced reduction in inorganic ion accumulation and increasing membranes stability and K^+/Na^+ ratio, enhanced chlorophyll formation and soluble sugar accumulation	[63]
	Salt	Alleviated salt stress by enhanced ethylene production	[64]

and IAA levels in tomato [35]. However, application of auxin completely reversed male sterility in barley and *Arabidopsis* [36]. The content of auxin was not affected by proline, but the expression of auxin carriers was reduced and in the overexpression lines of PDH, in which proline content was reduced, the expression of auxin carrier genes was induced [114].

3.4 Cytokinin

The exogenous application of CKs can mitigate the abiotic stresses on crop plants, which ultimately results in increased growth, development, and yield [52]. Likewise, supplementation of CKs also reduces salinity stress in plants [52], and it increases starch accumulation in salt-stressed rice plants [53] (Table 1). It has been reported that wheat seeds priming with kinetin (100 mg L^{-1}, 150 mg L^{-1}, and 200 mg L^{-1}) enhanced germination and tolerance against salt by decreasing ABA and increasing IAAs concentrations [54]. Likewise, Mangena [55] reported that soybean seed priming with CKs (Benzyl adenine; 4.87 mg L^{-1}) increased soybean root biomass, flowering, and fruiting under drought stress. Priming of aged groundnut (*Arachis hypogaea* L.) seeds with CKs (150 ppm) enhanced germination and seedling indices by enhancing antioxidant enzyme activities and decreasing oxidative damage [56]. Seed priming with CKs or a combination of CKs and other plant hormones has resulted in the mitigation of abiotic stresses in various plant species.

3.5 Gibberallin

Different abiotic stresses, such as salinity, drought, chilling, heat, and heavy metals, inhibit proper nutrient uptake and photosynthesis, which ultimately results in stunted plant growth [65]. The exogenous application of gibberallin can mitigate abiotic stresses and enhance plant growth and development (Table 2). Exogenous application of gibberallin improved the growth of wheat (*Triticum aestivum*) plants and mitigated drought induced oxidative damage by maintaining relative water content, balancing the antioxidant mechanism system, and conserving the chlorophyll concentration [66]. Foliar application of GA_3 @50ppm to tomato (*Solanum lycopersicum*) plants increased relative leaf water content, stomatal density, and chlorophyll content by mitigating salinity stress [67]. Besides, GA_3 was stimulated in plant growth and yield leaf of lettuce (*Lactuca sativa*) by enhancing biomass accumulation, leaf expansion, stomatal conductance, water use efficiency, and nitrogen use efficiency [68].

3.6 Abscisic acid

ABA is one of the major plant hormones and is also

Table 2. Seed-priming with gibberellin and response of plant species.

Plants	Stresses	Responses of Plant	References
Marigold and Sweet fennel	Salt	Increased dry matter and enhanced tolerance to salinity by enhancing antioxidant enzyme activities	[13]
Pigeon pea (*Cajanus cajan*)	Cadmium	Increased germination speed index and germination percentage and tolerance to Cd stress	[34]
Milk Thistle (*Silybum marianum*)	Salt	Increased α-amylase activity and alleviated salt stress effects	[37]
Chickpea (*Cicer arietinum*)	Drought	Increased relative water content, seed protein, and reduced electrolyte leakage	[38]
Wheat (*Triticum aestivum)*	Salt	Promoted better salinity tolerance	[39]
Sorghum (*Sorghum bicolor*)	Drought	Increased CAT and APX activities	[40]
Corn (*Zea mays*)	Salt	Increased tissue water content	[41]
Maize (*Zea mays*), Pea (*Pisum sativum*), Grass pea (*Lathyrus sativus)*	Salt	Alleviated salt stress effects	[42]
Rice (*Oryza sativa*)	Flood	Increased α-Amylase activity, sucrose, glucose, and fructose content in seeds.	[43]
Alfalfa (*Medicago sativa*)	Salt	Induced enzymatic activities (SOD, CAT, GPX, APX, GR) and decreased lipid peroxidation, and reduced membrane damage of alfalfa.	[44]
Sponge gourd (*Luffa aegyptiaca*)	Salt	Prevented the adverse effect of salinity	[45]
Soybean (*Glycine max*)	Saline-alkali	Increased activities of the antioxidant defense system, photosynthetic pigment contents, better membrane integrity	[46]
Maize (*Zea mays*)	Salt	Reduced negative effect of salt stress	[47]
Sweet sorghum (*Sorghum bicolor*)	Salt	Enhanced water absorption and improved salinity tolerance	[48]
Maize (*Zea mays*)	Drought	Increased chlorophyll content and enhance drought tolerance	[49]
Okra (*Abelmoschus esculentus*)	Salt	Increased water content of the okra seedlings	[50]
Triticale	Salt	Reduced Na^+ accumulation and increased K^+ uptake	[51]

known as a stress hormone. It plays a vital role in mediating plant responses to various abiotic stresses, such as salt, heat, and drought [69] (Fig. 3). ABA not only plays a role in abiotic stress mitigation but also plays a significant role in plant growth and development [70]. Rice seeds primed with ABA exhibited enhanced seedling growth and yield in saline soil by balancing nutrient uptake [71]. Likewise, priming rice seeds with ABA reduced alkaline stress by enhancing antioxidant enzyme activities and the activity of stress tolerance-related genes in the roots of rice seedlings [72]. It has been reported that phytohormones are effective in the mitigation of heavy metal stress [23]. ABA biosynthetic gene expressions are induced by heavy metal stresses, which results in increased levels of endogenous ABA [73]. Priming *Arabidopsis* seeds with amino-butyric acid enhanced drought tolerance by accumulation of ABA and the closing of stomata [74]. The regulation of proline metabolism is dependent on ABA accumulation [116], whereas other responses occur independently of ABA, and that ABA alone cannot duplicate drought-induced proline accumulation [117]. They proposed that GAs inhibited flowering and ABA promoted flowering in litchi [118].

3.7 Salicylic acid

Salicylic acid (SA) is a phenolic compound involved in the regulation of growth and development of plants, and their responses to biotic and abiotic stress

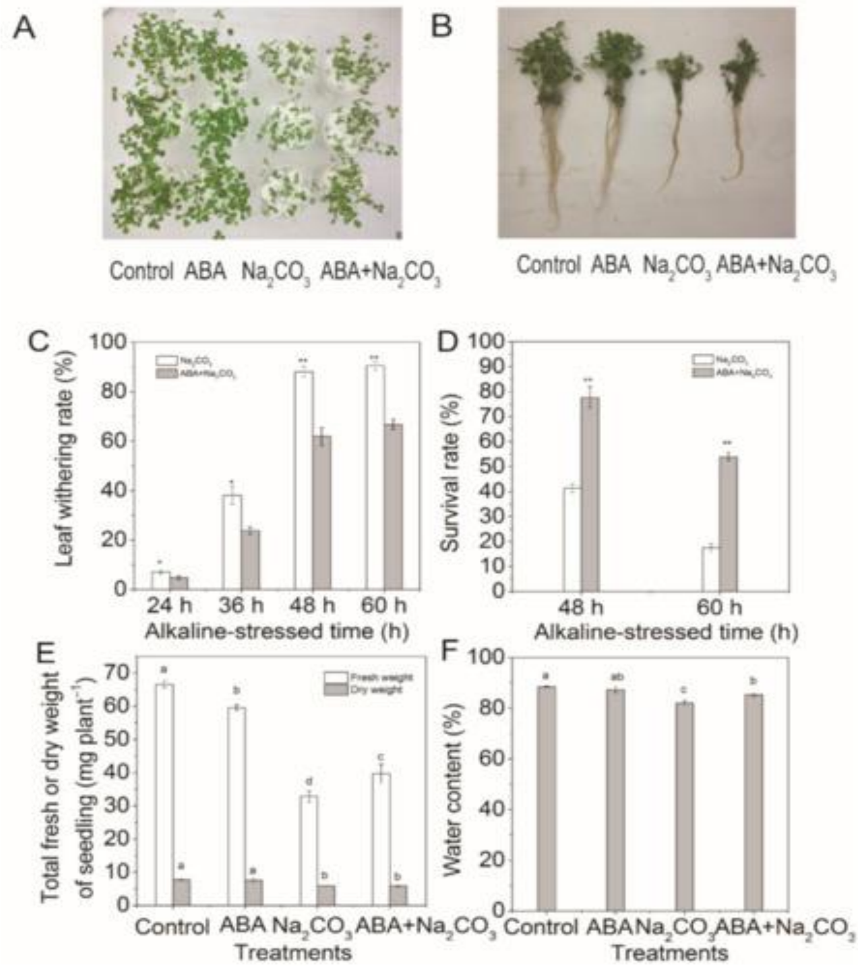

Figure 3. Abscisic acid (ABA) priming protected alfalfa (*Medicago sativa* L.) seedlings from wilting and death under alkaline conditions. Eighteen-day-old alfalfa seedlings were root-drenched with 10 µM ABA or without 10 µM ABA (Control) for 16 h and then exposed to alkaline stress (15 mM Na_2CO_3). (**A**, **B**) Photographs of seedling growth were taken after 60 h of alkaline treatment, (**C**) leaf withering (%) was recorded at 24 h, 36 h, 48 h, and 60 h, (**D**) survival rate of alfalfa seedlings was determined after 48 h and 60 h of alkaline treatment, (**E**) total fresh or dry weight of seedlings and (**F**) water content were measured after 60 h of alkaline treatment. Values are the mean ± standard error, n = 3. Asterisks denote a significant difference compared with control plants (* $p < 0.05$, ** $p < 0.01$) based on Student's *t*-test. Different letters above the columns indicate significant differences ($p < 0.05$) at each time point based on Duncan's test [112].

factors [75] (Table 3; Fig. 4). It is involved in the regulation of important plant physiological processes such as photosynthesis, nitrogen metabolism, proline metabolism, production of glycine betaine, antioxidant defense system, and plant-water relations under stress conditions and thereby protects plants against abiotic stresses [75]. SA has been shown to improve plant tolerance to major abiotic stresses such as metal [76], salinity [77], drought [78], and heat stress [79]. The exogenous application of salicylic acid enhanced maize (*Zea mays*) productivity under low temperature stress, as well as the germination and growth parameters of garden cress (*Lepidium sativum*) seedlings under salinity stress [80], and mitigated drought stress and enhanced the vegetative growth of

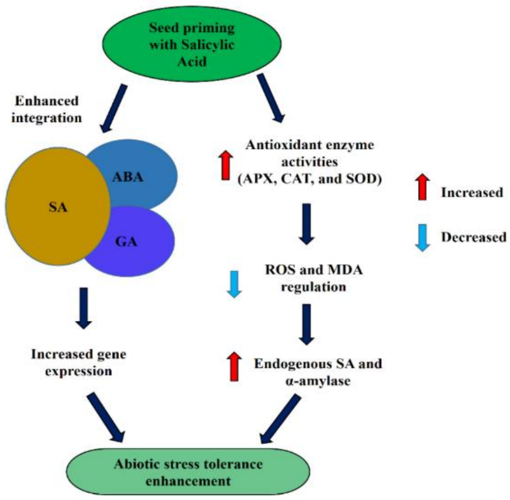

Figure 4. Mechanisms of SA priming for abiotic stress tolerance enhancement [24].

Table 3. Seed priming with salicylic acid and response of plant species.

Crops	Stresses	Responses of Plants	References
Rice (*Oryza sativa*)	Chromium	Increased chlorophyll content and proper nutrient uptake	[85]
	Water deficit	Decreased water stress	[86]
	Chilling	Enhanced antioxidant enzyme activities, detoxified ROS	[87]
	Salinity	Improved Na^+/K^+ and maintaining membrane integrity	[88]
Safflower (*Carthamus tinctorius*)	Drought	Enhanced antioxidant enzyme activities and reduced oxidative damage	[89]
Maize (*Zea mays*)	Chilling	Increased α-amylase and antioxidant enzyme activities and endogenous SA content	[90]
	Chilling	Enhanced enzymatic antioxidant activities, high tissue water content	[91]
	Lead	Increased glycine betaine and nitric oxide content and regulation of gene expression	[92]
	Chromium and UV-B	Reduced the accumulation of chromium and ROS	[93]
Wheat (*Triticum aestivum*)	Salinity	Decreased the electrolyte leakage	[94]
	Drought	Balanced nutrient uptake	[95]
	Osmotic	Resistance to osmotic stress	[96]
	Salinity	Higher contents of photosynthetic pigments, soluble sugar, and protein	[97]
	Boron toxicity	Increased photosynthetic pigments	[98]
	Cadmium	Modulates nutrient relations and photosynthetic attributes	[99]
Smooth vetch (*Vicia dasycarpa*)	Water deficit	Higher accumulation of proline and glycine betaine	[100]
Okra (*Abelmoschus esculentus*)	Chilling	Enhanced antioxidant enzyme activities and membrane integrity	[101]
Sorghum (*Sorghum bicolor*)	Drought	Improved antioxidant defense system	[102]
Tomato (*Solanum lycopersicum*)	Salinity	Decreased salinity stress	[103]
	Heat	Increased lycopene content	[104]
Pumpkin	Salinity	Protein contents and nitrate reductase were increased	[105]
Faba bean (*Vicia faba*)	Salinity	Higher osmotic solute content, carotenoids, and antioxidant enzyme activity	[106]

drought stress and enhanced the vegetative growth of safflower (*Carthamus tinctorius*) [81]. Priming with salicylic acid at 100 mg L^{-1} enhanced emergence and produced early seedling growth in cucumber (*Cucumis sativus*) [82] and increased germination and productivity of *Vicia faba* [83] and sesame (*Sesamum indicum*) [84].

3.8 Ethylene

Ethylene is regarded as a stress-responsive hormone besides its role in regulation of plant growth and development [107] (Fig. 5). The hydrocarbon ethylene is an important plant hormone and it is widely used for ripening fruits [108]. It was found that exogenous application of ethylene with sufficient sulphur level counteracted the cadmium-induced photosynthetic and growth inhibition in mustard plants [109]. Free proline content and ethylene production increase in cold-acclimated winter rapeseed seedlings under pretreatment with glutamine and especially with proline [115]. Free proline is involved in the response to cold stress, and its level may be an indicator of cold-hardening and freezing tolerance, but the role of ethylene in the regulation of cold tolerance remains not quite clear [115].

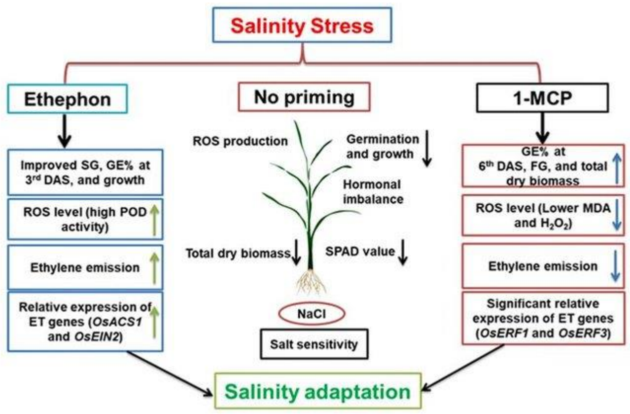

Figure 5. Ethylene response of salt stressed rice seedlings following Ethephon and 1-methylcyclopropene seed priming. SG= speed of germination, GE= germination energy percentage, 3rd and 6th DAS= 3rd and 6th day after sowing, and FG= final germination [113].

4. Conclusions

Seed priming with phytohormones has emerged as a promising strategy in modern stress management as it protects plants against various abiotic stresses by increasing level of antioxidant enzyme activity, decreasing oxidative damage, and enhancing plant growth. Thus, seed priming with phytohormones improves the tolerance of crop plants to abiotic stress, and this technique can be utilized to maintain sustainable crop production in drought-, saline-, and flood-prone areas of the world. Seed priming with phytohormones not only improves the tolerance to abiotic stresses but also ensures harmonized germination by breaking the dormancy and enhancing viability. This review provides insight into the role of seed priming with phytohormones in mitigating the effects of abiotic stress on seed germination and plant growth. Seed priming with phytohormones has emerged as an effective seed treating tool for many crops, but treating conditions and methods differ from crop to crop, and seed priming with phytohormones has still limitations. For instance, prolonged seed treatment with hormonal solution during priming may cause the loss of seed tolerance to desiccation, which reduces seed viability.

Authors' contributions

All authors equally contributed, read and approved the final manuscript.

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Conflicts of interest

There is no potential conflict of interest to describe.

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