**REVIEW**

Crop Economics, Production, and Management

# Hydrogen peroxide priming promotes salinity tolerance in plants—A comprehensive review

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**Abstract**

Salinity stress is a growing concern for agriculture, as soil salinization is increasing worldwide and seriously affects global agricultural production and food security. How to minimize the adverse effects of salinity stress and meet the food needs of the growing human population becomes an urgent problem. Conventional techniques in agriculture and recently modern plant science have limitations; therefore, alternative technologies such as hydrogen peroxide ($H_2O_2$) priming have emerged as promising solutions. The findings highlight that $H_2O_2$ priming enhances antioxidant defenses, regulating the balance between reactive oxygen species production and scavenging. Furthermore, $H_2O_2$ priming promotes osmotic adjustment by stimulating the accumulation of osmoprotectants, maintaining cellular water status under salinity conditions. The review also discusses how $H_2O_2$ priming modulates gene expression and signaling processes, causing stress-responsive genes and transcription factors activation. Moreover, $H_2O_2$ priming helps to preserve chloroplast integrity and photosynthetic efficiency, mitigating the detrimental impacts of salt stress on plant development and productivity. Overall, the collective knowledge gathered here, covering various aspects of the $H_2O_2$ priming phenomenon, may facilitate the design and conduct of future research on plant tolerance to salinity or other abiotic stresses. However, future research needs to focus on elucidating how priming can be applied on a large scale to diverse plants, understanding biochemical and molecular mechanisms of $H_2O_2$ priming for precise and reliable applications of this approach, and figuring out the potential benefits of in vitro priming ($H_2O_2$) technology in plant science.

## 1 | INTRODUCTION

Salinity stress is a growing concern for agriculture, as soil salinization is increasing worldwide due to various anthropogenic activities, such as irrigation with brackish water, the use of fertilizers containing high levels of salt, and land-use changes. Plants' osmotic, ionic, and nutritional balance can be affected by a high level of $Na^+$ and $Cl^-$ ions in the root zone (Cai & Gao, 2020). These modifications may inhibit growth

**Abbreviations:** ABA, abscisic acid; APX, ascorbate peroxidase; AsA-GSH, ascorbate-glutathione; ASC, ascorbic acid; CAT, catalase; ET, ethylene; GPX, glutathione peroxidases; GST, glutathione S-transferases; $H_2O_2$, hydrogen peroxide; JA, jasmonic acid; MAPK, mitogen-activated protein kinase; MDA, malondialdehyde; POD, peroxidase; PRX, peroxiredoxins; ROS, reactive oxygen species; SA, salicylic acid; SAM, S-adenosylmethionine synthetase 1; SI, sclerophylly index; SOD, superoxide dismutase; SUC, leaf succulence; WCS, water content at saturation; WSD, water saturation deficit.

and have an impact on various physiological processes. Both the photochemical and metabolic phases of photosynthesis may suffer under these circumstances (Melo et al., 2020). Besides, reactive oxygen species (ROS) generation and scavenging might become unbalanced as a result of salinity, which can lead to a high level of lipid peroxidation and a reduction in the integrity of cell membranes (A. Khan et al., 2019). Because ROS are extremely potent oxidizers and may respond to practically all components of live cells, causing significant damage to lipids, proteins, and nucleic acids, this tension (oxidative stress conditions) could result in cell damage (A. Khan et al., 2019). Therefore, there is a growing need for strategies to enhance plant resistance to salt stress.

$H_2O_2$ is an ROS that is generated in plants as a result of various stressors, including salinity stress. $H_2O_2$ acts as a signaling molecule controlling several biological functions, including cell proliferation, differentiation, and defense responses (X. Zhang et al., 2019). Priming involves the application of a sub-lethal dose of a stressor to plants before exposure to a lethal dose, which enhances their ability to cope with the stress. In recent years, researchers have investigated the potential of priming with low doses of $H_2O_2$ to increase resistance to salinity (Silva et al., 2020; H. Silva et al., 2019). A small number of research studies, however, describe how the standards for choosing doses for external use are determined and what the main processes are behind the increase in plant tolerance brought on by $H_2O_2$ priming.

The mechanisms underlying the priming of $H_2O_2$ in response to salt stress are complex and involve various physiological, biochemical, and molecular processes. Priming with $H_2O_2$ has been shown to enhance the activity of antioxidant enzymes, including catalase (CAT), peroxidase, and superoxide dismutase (SOD), which scavenge ROS and prevent oxidative damage to plant cells (Ellouzi et al., 2021; Hossain et al., 2015; Silva et al., 2020). Moreover, priming with $H_2O_2$ has been found to modulate the expression of genes associated with stress responses, like stress-related transcription factors, ion transporters, and osmoprotectants (Rossatto et al., 2017). In addition, $H_2O_2$ priming by improving the activity of carbon fixation enzymes, maintaining chloroplast architecture and carbon fixation along with the redox state in plants under salt stress, led to an increase in proteins related to photosynthesis and improved redox homeostasis (Araújo et al., 2021).

In the present study, in order to provide a comprehensive summary of the state of knowledge regarding $H_2O_2$ priming in the context of salinity stress in plants, the following topics were presented and discussed in order: (1) the physiological, biochemical, and molecular responses of plants to salinity stress with a focus on ROS production, especially $H_2O_2$, and the activity of stress response pathways; (2) summary of key findings of experimental and theoretical studies regarding the effects of $H_2O_2$ priming on plant development, photosynthe-

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**Core Ideas**

- $H_2O_2$ priming can regulate the antioxidant systems in plants.
- $H_2O_2$ priming can induce changes in stress-responsive genes.
- Finally, $H_2O_2$ priming improves plant tolerance to salinity stress.

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sis, and resistance to stress, as well as mechanisms beyond these effects; and (3) expressing the potential applications of $H_2O_2$ priming in typical agricultural practices, modern plant science, and the opportunities associated with this strategy, as well as addressing the challenges and barriers that prevent its widespread implementation.

It is worth noting that several reviews have been published in other journals that discuss the impact of hydrogen peroxide priming on enhancing plant resistance to abiotic stress, such as Johnson and Puthur (2021), Hossain et al. (2015), and Kerchev et al. (2020). Nevertheless, several features distinguished the present study from published reviews:

1. Focusing on $H_2O_2$ priming in response to salinity stress in seeds and seedlings of many plants.
2. Discussing the limitations and potential challenges associated with the use of the $H_2O_2$ priming strategy in agriculture to provide a more comprehensive view.
3. A description of how the $H_2O_2$ priming strategy can be integrated with genetic modification and other agronomic practices to provide valuable insights for clinicians and researchers.
4. Explaining the existence of a significant gap between research on $H_2O_2$ priming and its practical application in agriculture.

## 2 | THE ROLE OF $H_2O_2$ IN PLANT STRESS RESPONSES

$H_2O_2$ priming induces a controlled increase in endogenous $H_2O_2$ levels within plant cells, which acts as an indication to activate several defense mechanisms (Habib et al., 2020). High $H_2O_2$ concentrations have detrimental consequences, which are mostly a result of an all-pervasive oxidative stress response that damages cellular components regardless of their composition. Exogenous $H_2O_2$ is likely to trigger and/or alter additional ROS-producing systems, making it exceedingly difficult to distinguish between the harmful and signaling effects. The production of $H_2O_2$ is heavily compartmentalized between several cellular compartments and is influenced
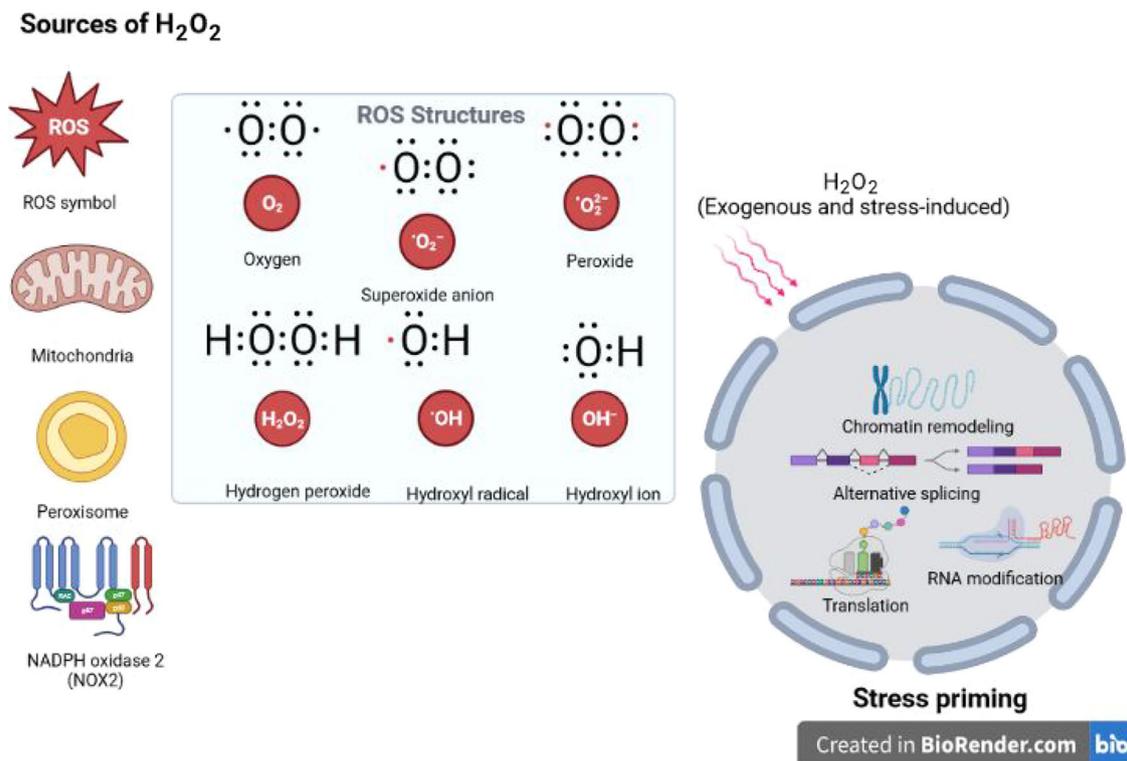
**FIGURE 1** Sources of $H_2O_2$ and potential use for stress adaptation. Different subcellular spaces create $H_2O_2$ in response to environmental cues and during regular metabolism. Significant physiological functions including gene expression, chromatin remodeling, alternative splicing, RNA modification and compartmentalization, and translation may be impacted by elevated $H_2O_2$ levels, which may eventually result in stress priming. ROS, reactive oxygen species.

by a variety of factors (Qureshi et al., 2022) (Figure 1). One of the key effects of $H_2O_2$ priming is the regulation of antioxidant systems in plants. $H_2O_2$ and other ROS are produced as a result of salinity stress within plant cells. ROS may result in oxidative damage to cellular components, such as proteins, lipids, and DNA (Hasanuzzaman et al., 2021). However, when plants are pre-treated with low levels of hydrogen peroxide through $H_2O_2$ priming, it triggers the upregulation of antioxidant enzymes, such as SOD, peroxidase (POD), CAT, the ascorbate-glutathione (AsA-GSH) cycle enzymes (ascorbate peroxidase [APX]), peroxiredoxins (PRX), glutathione peroxidases (GPX), and glutathione S-transferases (GST). These enzymes help scavenge excess ROS and protect the plant cells from oxidative damage (Hasanuzzaman et al., 2020). Non-enzymatic components such as GSH, ascorbic acid (ASC), $\alpha$-tocopherol, flavonoids, carotenoids, alkaloids, phenolic acids, and non-protein amino acids additionally have a crucial function in enhancing the plant's tolerance to stress in addition to enzymatic components (Hasanuzzaman et al., 2020).

Furthermore, $H_2O_2$ priming can regulate ion homeostasis in plants exposed to salinity stress. Salinity stress disrupts the balance of ions, particularly the excessive accumulation of sodium ions ($Na^+$) in plant tissues (Silva et al., 2020). This imbalance can be detrimental to normal cellular functions.

$H_2O_2$ priming activates ion transporters and channels, such as $H^+$-ATPase and SOS1, which play crucial roles in excluding $Na^+$ ions from the cytoplasm and reducing their toxicity. By regulating ion transporters, $H_2O_2$ priming helps plants maintain ion homeostasis and prevents the harmful effects of excessive sodium accumulation (Pandey et l. et al., 2021). In addition, $H_2O_2$ priming influences osmotic regulation in plants. Salinity stress leads to osmotic stress, where the high salt levels in the soil reduce water availability to plants. $H_2O_2$ priming enhances the aggregation of osmoprotectants, such as proline and soluble sugars, acting as compatible solutes. These osmoprotectants help plants maintain cellular osmotic balance, retain water, and protect proteins and membranes from damage caused by salinity stress (Koh et al., 2021).

Overall, $H_2O_2$ priming improves plant tolerance to salinity stress by activating antioxidant systems, regulating ion homeostasis, and enhancing osmotic regulation. It primes the plant's defense mechanisms and prepares them to better cope with subsequent salinity stress (Qureshi et al., 2022). Nevertheless, the efficiency of $H_2O_2$ priming can be different based on a number of parameters, including plant species, concentrations and timing of $H_2O_2$ application, and the severity of salinity stress. It is worth noting that the effectiveness of $H_2O_2$ priming may vary among different plant species and genotypes, as well as the concentration and

duration of the priming treatment. Further research is needed to optimize $H_2O_2$ priming techniques and understand the underlying molecular mechanisms involved in the responses of plants to salt stress.

## 3 | PRIMING AS A MECHANISM TO ENHANCE PLANT TOLERANCE TO SALINITY STRESS

### 3.1 | $H_2O_2$ priming and physiological and biochemical mechanisms under salinity stress

When plants are subjected to $H_2O_2$ priming before experiencing salinity stress, several physiological and biochemical responses are triggered to enhance their tolerance. The priming-related physiological and biochemical alternations help plants better respond to adverse impacts of salt stress. Several investigations on plants have shown that pre-treatment with a suitable concentration of $H_2O_2$ can increase abiotic stress resistance by modulating a variety of physiological processes, including photosynthesis (Hasan et al., 2016; M. I. Khan et al., 2016), and a variety of stress-responsive processes, including the ROS and methylglyoxal (MG) detoxification pathways (Gondim et al., 2012). Moreover, salinity stress often impairs photosynthetic efficiency in plants due to the disruption of chloroplast function (Hameed et al., 2021). $H_2O_2$ priming can help lessen the negative impacts of salt stress on photosynthesis. It enhances the activity of photosynthetic enzymes, such as ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), and the efficiency of carbon fixation (Chaves et al., 2009). The fact that $H_2O_2$ treatments raised the maximum carboxylation rate of Rubisco (V cmax) and initial Rubisco activity but had no impact on Rubisco's overall function may be the cause of the $H_2O_2$-mediated improvement in photosynthesis effectiveness. This suggests that Rubisco's activity status is primarily regulated by $H_2O_2$, potentially by the Rubisco enzyme (Jiang et al., 2012). As a result, $H_2O_2$-primed plants maintain higher photosynthetic rates and accumulate more carbohydrates, which is crucial for growth and stress tolerance (S. Wang et al., 2022). In support of these findings, Jiang et al. (2012) determined the involvement of $H_2O_2$ on carbohydrate metabolism. This study showed that the increases in carbohydrate metabolite content were accompanied by increases in the activity of sucrose synthase and acid invertase activity (AI) and the activity of sucrose synthase in $H_2O_2$-treated leaves, which increased by 23% and 116%, respectively.

$H_2O_2$ priming also activates the antioxidant defense system in plants. It enhances the activity of antioxidant enzymes, including SOD, CAT, and PODs (Bagheri et al., 2019). These enzymes scavenge excess ROS, including hydrogen peroxide, and minimize oxidative damage to cellular components (Ellouzi et al., 2021). The enhanced antioxidant capacity helps maintain cellular redox balance and protects plants from oxidative stress caused by salinity (Ellouzi et al., 2021). Besides, ROS can be quenched by non-enzymatic compounds including carotenoids, flavonoids, reduced glutathione, ASC, and suitable osmolytes such as proline, glycine betaine, and trehalose sugar (M. I. Khan et al., 2015; Per et al., 2017). Therefore, $H_2O_2$ priming improves water status and osmotic adjustment mechanisms. It promotes the aggregation of compatible solutes such as proline, soluble sugars, and other osmolytes (Karimi et al., 2020). These osmoprotectants help maintain cellular osmotic balance, reduce water loss, and protect cells from the damaging effects of salt stress (Terzi et al., 2014). On the other hand, salinity stress disrupts ion homeostasis by causing $Na^+$ and $Cl^-$ ion accumulation in plant tissues. $H_2O_2$ priming enhances the expression and activity of ion transporters, such as $H^+$-ATPase and SOS1, which facilitate the efflux of $Na^+$ ions and maintain ion homeostasis. By regulating ion transport, $H_2O_2$-primed plants can minimize the toxic effects of excessive $Na^+$ accumulation and maintain cellular ion balance (Chattha et al., 2022; Silva et al., 2020). $H_2O_2$ priming can also trigger the synthesis of secondary metabolites, including phytohormones, phenolic compounds, and flavonoids (Karimi et al., 2020; W. Wang et al., 2022). These metabolites play crucial roles in plant defense against salinity stress. They act as signaling molecules, enhance antioxidant capacity, scavenge free radicals, and regulate various physiological and biochemical processes involved in stress tolerance (Kesawat et al., 2023). Furthermore, $H_2O_2$ links the signaling processes of several phytohormones; this link was initially discovered between $H_2O_2$ and ethylene (ET). In addition to ET, $H_2O_2$ is very intimately associated with other important phytohormones, including abscisic acid (ABA), jasmonates, ET, and salicylic acid (SA). To coordinate stress reactions, plant development, and growth, all of these phytohormones need $H_2O_2$ in their signaling pathways, either upstream or downstream (Saxena et al., 2016).

Sunflower plants were able to produce more dry mass in all areas of the plant when 1 mM $H_2O_2$ was sprayed on the leaves 48 h before salt stress exposure. This improved the plants' resistance to salt stress. Due to stomatal restriction, salt-stressed sunflower plants did not experience a decrease in growth or net $CO_2$ assimilation rates (Silva et al., 2020). The major cause of the decline in growth and photosynthesis, however, may have been the rise in the harmful ions ($Na^+$ and $Cl^-$) levels. Studies confirm that the buildup of $Na^+$ and $Cl^-$ in photosynthetic tissues can be directly linked to the lowering of the RuBisCo carboxylation efficiency (Melo et al., 2020). It appears that $H_2O_2$ could activate physiological processes for $Na^+$ and $Cl^-$ exclusion and decrease in $K^+$ outflow from tissues, increasing the ion homeostasis and enhancing the resistance to salinity in sunflower plants (Silva et al.,

2020). This is supported through a reduction in $Na^+$ (40%) and $Cl^-$ concentrations (42%) and an elevation in $K^+$ levels (29% and 59%) either in leaves or roots in $H_2O_2$-primed plants compared to non-primed plants.

According to certain research, $H_2O_2$ can cause plants under salt stress to have a higher $K^+/Na^+$ ratio and a lower $Cl^-$ content (H. Silva et al., 2019). A method to preserve plants under salinity may be thought of as the pronounced rise in the levels of soluble carbohydrates, free amino acids, and free proline salt-induced in the leaves and roots of non-primed plants (Reddy et al., 2017). According to a previous study, during salt stress, plants accumulate low-molecular-mass organic molecules whose major activities are to maintain water status, shield cells from oxidative damage, and serve as signaling factors (Azevedo et al., 2009).

According to A. Khan et al. (2019), a variation in redox homeostasis, which characterizes oxidative tension, might result from this rise in ROS generation and cause problems with cell structure and metabolism. By increasing the antioxidant enzymes, such as SOD, CAT, APX, guaiacol peroxidase, and others, $H_2O_2$ priming, on the other hand, induces an increase in anti-oxidant activity (de Azevedo Neto et al., 2005; Gondim et al., 2012; Hossain et al., 2015). One of the most important strategies to lessen the detrimental impacts of salinity is an increase in the production of these enzymes, which can considerably be associated with the preservation of redox equilibrium (de Azevedo Neto et al., 2005). Catalase stands out among the antioxidant enzymes due to the substantial rise in its activity in either leaves or roots over the two assessment stages. The findings of the current investigation support the hypotheses put out by de Azevedo Neto et al. (2005) and Gondim et al. (2012) that the ROS-detoxifying process, which is aided by the increase in CAT activity brought on by $H_2O_2$ priming, increases the susceptibility of plants to salinity stress.

According to previous findings, researchers investigated the effect of $H_2O_2$ priming on cauliflower seeds and seedlings under salinity stress. The researchers found that $H_2O_2$ priming enhanced the antioxidant defense system, improved osmotic adjustment, and increased stress recovery capacity in cauliflower seeds and seedlings. They concluded that $H_2O_2$ priming could improve plant resistance to salinity stress (Ellouzi et al., 2021). A study focused on the impact of $H_2O_2$ priming on wheat seedlings under salinity stress. The researchers found that $H_2O_2$ priming enhanced antioxidant enzyme activities, such as SOD, CAT, and POD, and elevated the accumulation of non-enzymatic antioxidants, such as ascorbate and glutathione in wheat (*Triticum aestivum* L.) (Abdel Latef et al., 2019). These changes helped alleviate oxidative damage caused by salinity stress. The researchers observed that $H_2O_2$ priming enhanced the activity of antioxidant enzymes, such as SOD, CAT, and APX, and increased the levels of non-enzymatic antioxidants, including ascorbate

and glutathione. $H_2O_2$-primed plants also exhibited improved $Na^+/K^+$ ratio, indicating better ion homeostasis. The study concluded that $H_2O_2$ priming improved resistance to salinity in wheat plants by modulating antioxidant defenses and ion homeostasis (Abdel Latef et al., 2019).

A recent research also demonstrated that the salt stress decreased the relative water content, water saturation deficit (WSD), water content at saturation (WCS), leaf succulence (SUC), and sclerophylly index (SI) in the leaves for the non-primed treatment with $H_2O_2$. In contrast, $H_2O_2$ priming enhanced the plants' water status and decreased water loss, as seen by an elevation in WSD (53% and 20%) and WCS (39% and 63%) compared to control plants. Increased leaf thickness is indicated by high SI values (53% compared to non-primed plants) (Silva et al., 2020). According to some studies, a rise in SI is a process designed to improve the leaf's resistance to water diffusion and, as a result, reduce water losses (Cunningham & Strain, 1969). As a result of this process, SUC, a variable that represents the quantity of water per unit leaf area, also rises. Silva et al. (2020) reported that in two evaluation periods, salinity stress increased the SUC of sunflower plants compared to control plants. For the same periods, the increase in SUC of $H_2O_2$-primed plants was 30% and 28%. According to some authors, an increase in SUC can be a significant mechanism for the dilution of harmful ions in addition to sustaining water storage (Cova et al., 2016; H. Silva et al., 2019). Furthermore, maize plants that had been $H_2O_2$ pretreated had better photosynthetic performance, preventing salinity-induced surplus energy and ultrastructural damage by maintaining stacking thylakoids. The alteration of several metabolites, including arabitol, glucose, asparagine, and tyrosine, was seen. These metabolites may help to keep osmotic equilibrium and lessen oxidative tension (dos Santos Araújo et al., 2021). Recent research findings demonstrated that under salinity conditions, the level of malondialdehyde (MDA) in Arabidopsis seedlings that had been pretreated with $H_2O_2$ was significantly lower compared to non-pretreated seedlings, demonstrating that $H_2O_2$ pretreatment can effectively mitigate the damage of salinity stress with the stability and consistency of the membrane within cells of plants (Q. Zhang et al., 2022). As a result, to preserve development under salinity stress and enhance Arabidopsis seedlings' resistance to salinity, $H_2O_2$ plays a protective role which has been observed in other studies (de Azevedo Neto et al., 2005; Fedina et al., 2009; Gondim et al., 2012; Y. Wang et al., 2010). According to Sathiyaraj et al. (2014), *Panax ginseng* seedlings exposed to $100 M H_2O_2$ for 2 days demonstrated improved salt tolerance as well as higher APX, CAT, and guaiacol peroxidase activities. In $H_2O_2$-treated salt-stressed seedlings, other oxidative metrics including MDA levels, endogenous $H_2O_2$ levels, and $O^{-2}$ levels were reduced. Once seedlings were exposed to salinity, $H_2O_2$-treated seedlings had higher seedling dry weight and chlorophyll and carotenoid concentrations

than untreated controls. The aforementioned results show that $H_2O_2$ priming can improve plant growth and development by modifying physiological and metabolic processes such photosynthesis, proline accumulation, and ROS detoxification. This can help plants become more tolerant to salt stress (Sathiyaraj et al., 2014). In another experiment, researchers discussed how $H_2O_2$ helped wheat (*T. aestivum* L.) plants cope with salt stress. Plants treated with $H_2O_2$ grew more successfully in both saline and non-saline environments. The addition of 50 or 100 M $H_2O_2$ decreased the severity of salt stress, resulting in lower levels of $Na^+$ and $Cl^-$ ions as well as an increased amount of proline and N absorption. When compared to untreated plants, $H_2O_2$ under salt stress showed increased water relations, higher photosynthetic pigments contents, and faster growth rates. The treatment of $H_2O_2$ in non-saline circumstances also enhanced all of the aforementioned metrics. For wheat plants cultivated in non-saline settings, treatment with 100 M $H_2O_2$ offered the greatest protection, and it significantly reduced the impacts of salinity on plants produced in saline environments (Ashfaque et al., 2014).

These studies demonstrate the potential of $H_2O_2$ priming to improve plant resistance to salt stress by regulating physiological and biochemical responses. However, it is essential to remember that the specific experimental conditions and plant species used in these studies may influence the observed effects. More investigation is required to explore the efficacy of $H_2O_2$ priming in various plant species and under various salinity stress conditions.

It is important to note that the effectiveness of $H_2O_2$ priming and the specific physiological and biochemical responses may vary depending on various factors, such as plant species, concentration and duration of priming, and severity of salinity stress. Furthermore, the signaling pathways and molecular mechanisms underlying these responses are still being elucidated through ongoing research. Therefore, $H_2O_2$ priming holds promise as a master plan to enhance the resistance of plants to salinity stress by modulating physiological and biochemical responses that mitigate the negative effects of salinity. Continued research in this field can provide further insights into the specific mechanisms involved and optimize $H_2O_2$ priming techniques for different plant species and salinity conditions.

## 3.2 | $H_2O_2$ priming and molecular mechanisms under salinity stress

$H_2O_2$ priming can trigger changes in gene expression patterns, leading to the upregulation of stress-responsive genes (Mittler, 2002). It enhances the expression of genes encoding various stress-related proteins, including transcription factors, chaperones, and detoxification enzymes (Y. Cheng & Song, 2006; González et al., 2012). On the other hand, this

ROS interacts with additional signal molecules and pathways and also plays a role in regulating downstream genes (Neill et al., 2002). For instance, the downstream of $H_2O_2$, mitogen-activated protein kinase (MAPK) pathways seem to work. In plants, MAPK constitutes a sizable system involved in several processes, including the transmission of $H_2O_2$ signals (Xing et al., 2008; A. Zhang et al., 2006). Accordingly, $H_2O_2$ activates nicotiana protein kinase 1 in a MAPK cascade, which mimics the $H_2O_2$ effect and initiates the MAPK cascade that induces specific stress-responsive genes (Desikan et al., 2001; Grant et al., 2000; Kovtun et al., 2000). Even when given to the roots, $H_2O_2$ quickly activates MAPKs in the shoots (Capone et al., 2004). According to studies, $H_2O_2$ regulates seed germination and dormancy by causing the activation of ABA catabolism genes (X. M. Liu et al., 2010). The regulation of ROS-related defense genes often involves the zinc-finger transcription factor. In response to $H_2O_2$ and methyl viologen treatment, it was shown that the ZAT7 and ZAT12 zinc-finger proteins of Arabidopsis are substantially increased by oxidative stress in apx knockout mutants (Rizhsky et al., 2004). Under salt stress, ZAT10 functions both as a repressor and an inducer of ROS-responsive genes (Sakamoto et al., 2004). By altering ROS concentrations and SA-related gene expression, ZAT6 positively affects resistance to salinity in addition to tolerance to bacterial infection (Shi et al., 2014). According to a proposed model of the $H_2O_2$ signaling process, a cell surface receptor may detect an $H_2O_2$ signal, which might lead to an increase in $[Ca^{2+}]$cyt. A signaling protein, such as a protein kinase or phosphatase, could be activated by the elevated concentration of $[Ca^{2+}]$cyt, resulting in a cascade that mediates the phosphorylation or dephosphorylation of a transcription factor. Furthermore, $H_2O_2$ can directly oxidize transcription factors that are $H_2O_2$-responsive through the oxidation of cysteine residue thiols in proteins. The changed (activated) transcription factor enters the nucleus where it binds to the target promoter's matching cis-acting region to control gene expression (T. A. Khan et al., 2018). According to transcriptional research, exogenous $H_2O_2$ pretreatment induces the expression of genes associated with the cell cycle (*CYCs*, *CDKB1;2*, *CDKB2;1*, their upstream regulator *DEL1* and its target *CDT1A*, as well as *MCM2*, *MCM3*, and *MCM6*), redox regulation (*TT4*, *CRWN2*, *CRWN3*, *CRWN4*, *ACS6*, *SOS6*, *RBOHD*, *VTC2*, *FSD3*, *GPX7*, and *GSTU24*), and cell wall organization (mitosis kinases, MAPs, kinesin superfamily, chromosome organization proteins, and kinetochore complex) in Arabidopsis. These genes could speed up cell division, increase sensitivity to osmotic stress, maintain redox balance, and modify plant cell walls following high-salt conditions (Q. Zhang et al., 2022). Both cell proliferation and chromosomal structure can be preserved by these cell cycle genes. Since cell division and growth are the primary factors that drive plant growth, increased levels of these genes could allow the preservation of plant development in dealing with

the ensuing stresses, as demonstrated in numerous studies. For instance, the overexpression of the genes *CYCB1;1* and *CYCB2;2* in rice plants resulted in accelerated plant development (Lee et al., 2003), and *MCM6* might have a function in the normal progression of DNA replication, thereby granting transgenic tobacco resistance to salinity (Dang et al., 2011). These results offer compelling evidence that resistance to salinity and plant development were both improved by $H_2O_2$ pretreatment. However, it is still unknown how low amounts of $H_2O_2$ enhance plant growth and cell cycle advancement. Moreover, it was suggested that pre-treatment with $H_2O_2$ led to an increase in the levels of ROS-scavenging enzymes and the expression of the genes for pyrroline-5-carboxylate synthase, sucrose-phosphate synthase, and small heat shock protein 26. These results suggest that nitric oxide (NO) and $H_2O_2$ function as signaling molecules that alter the tolerance to heat and salinity stress by controlling the expression of genes relevant to stress (Uchida et al., 2002).

$H_2O_2$ priming can influence hormone signaling pathways under salinity stress. It may enhance the expression of genes associated with stress-responsive hormones, including ABA, ET, SA, and jasmonic acid (JA), which play crucial roles in stress signaling and tolerance. Additionally, it may impact the expression of genes associated with hormone secretion, metabolism, and signaling cross-talk (Saxena et al., 2016). A recent study, in Arabidopsis, found that numerous genes related to hormone manufacture or connected signaling processes were upregulated in response to $H_2O_2$ pretreatment. The earliest steps of ABA and ET biosynthesis are aided by *ABA1* and *ACS6*, while *ABA3*, *ABI2*, *ERF1*, *ERF4*, *ERF6*, *ERF106*, *MYB51*, *WRKY70*, and *VSP1* are involved in the transduction of ABA, ET, or JA signals (Q. Zhang et al., 2022). Besides, $H_2O_2$ pretreatment led to the induction of *RBOHD*, a significant member of the RBOH family. In the response of phytohormones and $H_2O_2$ to diverse environmental stimuli, *RBOHs* have been identified as significant targets (Yao et al., 2017).

Under $H_2O_2$+salt stress treatment, Arabidopsis also exhibited a strong concentration of upregulated osmotic stress-responsive genes. *P5CS1* encodes a crucial enzyme in proline biosynthesis to enhance the accumulation of proline, while *RD29A* and *RD29B* encode hydrophilic proteins that function as protective molecules under osmotic tension (Feng et al., 2016). On the other hand, studies showed that high salinity followed by a low level of $H_2O_2$ pretreatment, either separately or together, promoted the expression of cell wall remodeling genes. The class B endoglucanases *AtGH9B1*, *AtGH9B8*, and *AtGH9B13* and the class C endoglucanase *AtGH9C2* all control the production of cellulose. It has been demonstrated that upregulating *FUT4* thickens plant cell walls and improves plant salt tolerance which is responsible for fucosylating *AGPs* in leaves (Tryfona et al., 2014). Figure 2 provides a summary of the connections between $H_2O_2$ sig-

naling and molecular mechanisms. This figure illustrates the complex interactions between $H_2O_2$ signaling, environmental and metabolic stimuli, their aftereffects, and plant growth. It seems that the signaling, growth, stress responses, and stress tolerance of plant cells appear to be influenced by $H_2O_2$.

Regarding the proteomic changes in response to $H_2O_2$ priming, different mechanisms have been reported. First, it may induce the upregulation or downregulation of specific proteins involved in stress response, such as antioxidant enzymes, ion transporters, osmoprotectant synthesis enzymes, chaperones, and stress signaling components. These differentially expressed proteins contribute to improved salinity stress tolerance. In a study on maize, $H_2O_2$ priming resulted in the upregulation of several stress-related proteins, including SOD, peroxidase, APX, and heat shock proteins. These proteins play crucial roles in antioxidant defense, stress signaling, and protein protection (Araújo et al., 2021). Through targeted proteome reprogramming, $H_2O_2$ priming in maize improved shoot development by increasing dry mass by 61% and improved responsiveness to salinity by a 16% reduction in $Na^+$ concentration. The proteins were linked to photosynthesis, redox homeostasis, and state redox, which are vital metabolic processes for preserving chloroplast organization and carbon fixation in plants under saline stress (Araujo et al., 2021). Citrus plants' ability to survive high salinity was improved by pre-treating them with $H_2O_2$ or SNP. The findings revealed interactions between $H_2O_2$ and NO-signaling processes in plants under NaCl stress and added evidence to the notion that both of these molecules act as priming-active molecules to trigger systemic adaptation against salt. Citrus NaCl-stressed leaves were demonstrated to result in a particular proteome reprogramming following $H_2O_2$ or SNP pre-exposure, which allowed avoiding the aggregation of a significant number of NaCl-responsive proteins and most likely accounted for the observed phenotypes. Furthermore, it appears that a crucial mechanism by which $H_2O_2$ and NO set the citrus plant up to enhance the plant's ability to cope with salinity stress is the control of protein carbonylation and S-nitrosylation (Tanou et al., 2009).

A short oxidative burst from $H_2O_2$ priming may stimulate signaling pathways in plants, causing an accumulation of latent defense proteins that puts the plant in a primed condition and makes it more resistant to stress in the future (Hossain et al., 2015). It is noteworthy that $H_2O_2$ priming also increased the expression of a P-protein called the glycine cleavage complex that is crucial for C3 plants' photorespiration (Araujo et al., 2021). Furthermore, the buildup of essential proteins, such as stress-responsive proteins, suggests that $H_2O_2$ priming could function as a stress elicitor in maize leaves, which is not surprising given that $H_2O_2$ participates in signaling biotic and abiotic stimuli and modulating phytohormone activity (Černý et al., 2018). In plants exposed to salinity, $H_2O_2$ priming increased the expression of
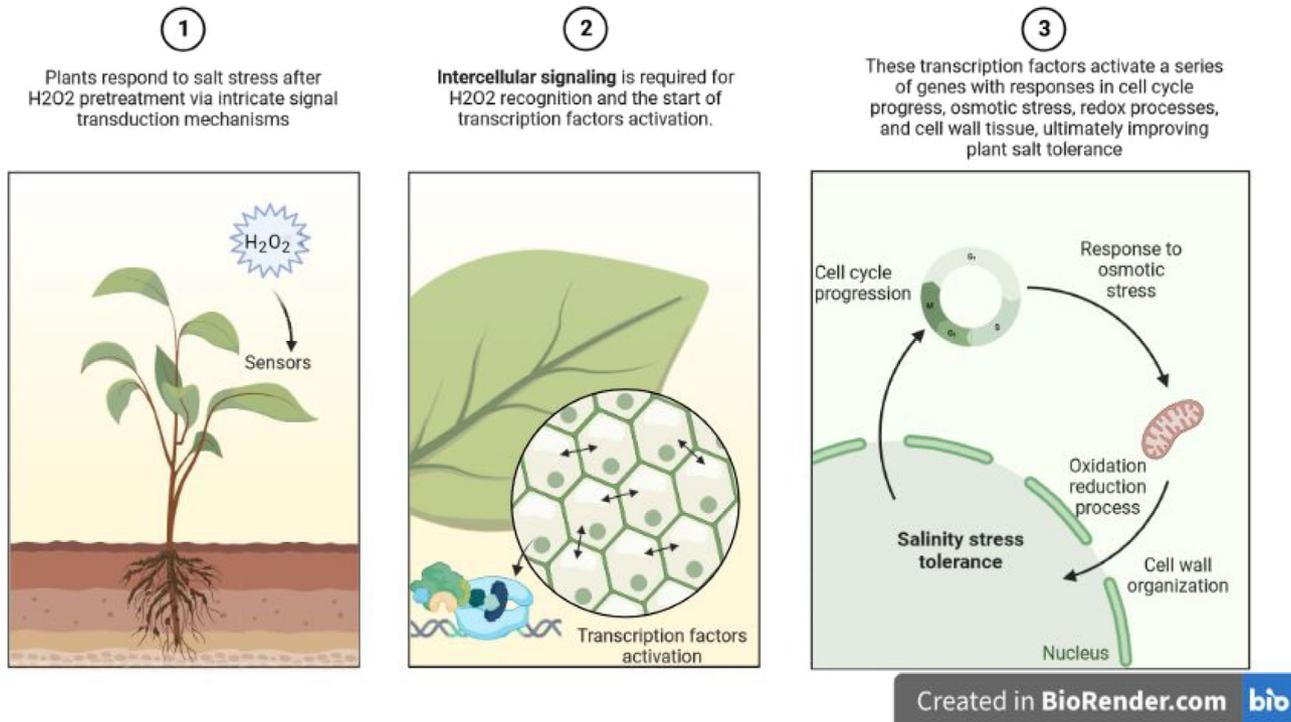
**FIGURE 2** A graphic depiction of the main molecular mechanisms in response to $H_2O_2$ treatment and how they could improve salinity stress tolerance.

proteins involved in $CO_2$ assimilation, such as ribulose 1,5-bisphosphate carboxylase and rubisco large subunit-binding protein subunit alpha. As a result of the overexpression of these proteins in maize plants, photosynthesis was improved (Dos Santos Araújo et al., 2021), and the increased growth led to reduced salt effects (Salesse-Smith et al., 2018). After fruit protein pKIWI502 was upregulated, the plants pretreated with $H_2O_2$ also displayed an adjustment in redox homeostasis proteins. Besides, modifications were implemented to the ferredoxin isoforms through upregulation, downregulation, and repression of the ferredoxin (Araújo et al., 2021). On the other hand, $H_2O_2$ priming maintained the majority of proteins that were elevated through salt stress, decreasing the expression of only cysteine synthase and increasing the expression of S-adenosylmethionine synthetase 1 (SAM), a stress response protein required for the production of S-adenosylmethionine from methionine and ATP. In addition to regulating reactions to abiotic stressors, SAM functions as a precursor for the manufacture of polyamines (Saha et al., 2015). Accordingly, increased photosynthetic rates and biomass buildup caused by overexpression of the S-adenosylmethionine synthetase gene have been directly linked to improved resistance to salinity (Ma et al., 2017). Furthermore, because it contains a large family of RNA-binding proteins linked to mRNA metabolic processes in addition to a variety of functions including DNA repair, chromatin remodeling, telomere biogenesis, cell signaling, and development regulation, the ribonucleoprotein de novo synthesized could result in a better response to environ-

mental stress (Ciuzan et al., 2015). Moreover, the increased putative plastid-lipidassociated protein 2 can shield plants from stress by reducing the oxidation of thylakoid membranes (Tamburino et al., 2017). Three-phosphoglycerate kinase and triosephosphate isomerase, two proteins linked to the glycolytic and metabolic procedures, were downregulated by $H_2O_2$ priming in maize plants during salinity in order to modify energy metabolism. Similar to sensitive plants, which need to produce large amounts of ATP to tolerate stress, abiotic stress-tolerant plants aggregated fewer proteins associated with energy metabolism (L. Cheng et al., 2016). Therefore, the $H_2O_2$ priming reduced the negative impacts of salinity by enhancing carbon assimilation-related proteins, conserving energy, and maintaining homeostasis redox in maize plants (Araújo et al., 2021). Table 1 summarizes a list of dysregulated proteins involved in response to $H_2O_2$ priming under salinity stress.

## 3.3 | Applications of $H_2O_2$ priming in conventional agriculture

In recent decades, the use of $H_2O_2$ priming to mitigate the effects of salinity stress in agriculture by different pathways has been the focus of researchers as an alternative/novel technique. Tania et al. (2022) reported that $H_2O_2$ priming can enhance the stress tolerance of kidney bean by activating various protective mechanisms. In sunflower, the findings

**TABLE 1** A list of dysregulated proteins involved in response to $H_2O_2$ priming under salinity stress.

| Protein category | Subgroups |
| --- | --- |
| Photosynthesis/ carbon metabolism | Rubisco, large subunit, partial |
| | Rubisco, large subunit- binding protein, subunit alpha |
| Energy metabolism | 3-Phosphoglysrate kinase, partial |
| | Triosephosphase isomerase |
| | Malate dehydrogenase |
| Redox homeostasis | Ferredoxin |
| | Fruit protein pKIWI502 |
| Response to stress | S-Adenosylmethionine synthetase 1 |
| | Cystein synthase |
| RNA metabolism | Rhibonucleoprotein |
| Unknown proteins | Putative plastid lipid-associated protein 2 |

of Silvia et al. (2020) showed that this technique promotes antioxidant defense systems, ion homeostasis, osmotic regulation, and stress signaling pathways and ultimately leads to improved plant performance under salinity stress conditions. Indeed, the findings showed that by maintaining normal physiological functions, enhancing plant adaptation, and subsequently improving stress tolerance, $H_2O_2$ priming has the potential to increase the quality and quantity of crops and decrease the detrimental effects of salt stress in saline environments (Shively et al., 2013; Silva et al., 2020).

There are also challenges associated with $H_2O_2$ priming for salinity stress in agriculture. In this regard, determining the appropriate concentration and timing of $H_2O_2$ priming is crucial. While low concentrations of $H_2O_2$ can induce stress tolerance, excessive concentrations can have detrimental effects on plant growth and cellular functions (Silva et al., 2020). Fine-tuning the priming conditions is necessary to ensure optimal results. Moreover, the response to $H_2O_2$ priming can vary among different plant species and cultivars. Some plants may exhibit better priming responses than others. For example, studies have shown that the exogenous application of 10 mM and 160 μM $H_2O_2$ solution as a priming agent induces tolerance to salinity stress in maize leaves and milk thistle (*Silybum marianum*) seeds, respectively. Therefore, it is essential to identify suitable crop varieties and assess their responsiveness to $H_2O_2$ priming under salinity stress. Environmental factors, such as temperature, humidity, and light intensity, can also influence the effectiveness of $H_2O_2$ priming. These conditions should be carefully considered and controlled to maximize the benefits of priming in agricultural settings. Information about the concentration and time of priming plants with $H_2O_2$, the positive effects, and the mechanism of positive effects of hydrogen peroxide in alleviating the detrimental effects of salinity stress in several plants are presented in Table 2.

In summary, $H_2O_2$ priming can be integrated with other agronomic practices and stress management strategies to enhance salinity stress tolerance further. Combining priming with proper irrigation techniques, soil amendments, and genetic approaches can potentially result in synergistic effects and better crop performance under salinity conditions. The development of commercially available $H_2O_2$ priming products can provide a practical and convenient solution for farmers. These products can be formulated to ensure optimal concentration and stability, making them easier to use and apply on a large scale. Further research on the molecular mechanisms underlying $H_2O_2$ priming can open new avenues for improving crop tolerance to salinity stress. Investigating the specific genes, proteins, and signaling pathways involved in the priming process can lead to the development of targeted strategies for crop improvement.

## 3.4 | Applications of $H_2O_2$ priming in modern plant science and related technologies

In plant breeding programs and genetic engineering (e.g., transgenic technology, gene mutation, and polyploidy breeding), future opportunities associated with $H_2O_2$ priming should not be declined. Tissue culture as one of the necessities of breeding and genetic engineering programs can be introduced as one of the application fields of priming programs for future studies because priming can be applied to organs or their fragments excised from donor plants using in vitro culture (Wiszniewska, 2021). Such a method is relatively labor-consuming and requires the necessary laboratory equipment to establish propagating cultures. However, an unavoidable advantage of this approach is the possibility of a large-scale screening of priming compounds according to their forms or concentration (Moghanloo et al., 2019). In fact, tissue culture conditions can be considered a stressful environment, so priming can induce and maintain reproductive activity, improve plant growth and tolerance, improve seedling emergence and performance, and reduce the possible risk caused by environmental factors and efficient regeneration, especially in endangered species (Singh et al., 2015). Moreover, priming can be done in the form of specific manipulations during cultivation, the use of chemical compounds in the culture medium or pretreatment of the explant before the start of cultivation, or in the form of biotization of the culture with growth-stimulating microorganisms (Nowak & Shulaev, 2003). Another main purpose of in vitro priming is to stimulate the morphogenetic responses of explants as well as the synthesis and release of biologically active compounds (Rezaei et al., 2018).

The success of in vitro priming using priming agents of physical, chemical, and biotic natures by inducing oxidative bursts or regulating key genes of secondary metabolites

**TABLE 2**    Information about the concentration, time of priming plants with $H_2O_2$, and the positive effects and the mechanism of these effects in alleviating the detrimental effects of salinity stress.

| Plant | Concentrations of $H_2O_2$/duration of treatment | Positive effects | Mechanisms | Type of priming | Reference |
|---|---|---|---|---|---|
| *Silybum marianum* | 160 μM/8 h | Increasing growth, development, and salinity tolerance in primed plants. | Improvements in physiological attributes. | Seed priming by $H_2O_2$ | Migahid et al. (2019) |
| *Brassica oleracea* | 120 μM/12 h | Increasing the level of seed superoxide anion (fivefold), $H_2O_2$ (fourfold), and MDA content (2.4-fold) at the primed seedlings and triggering the overall seedling antioxidant defense, including enzymatic (SOD, CAT, GPX, and APX) and non-enzymatic systems (AsA, GSH, and proline). | Stimulating the antioxidant system and maintaining the redox balance. | Seed priming by $H_2O_2$ | Ellouzi et al. (2021) |
| *Zea mays* | 10 mM/24 h | Modulation of some metabolites such as arabitol, glucose, asparagine, and tyrosine to the maintenance of osmotic balance and oxidative reduction, maintenance and enhancing the efficiency of photosynthetic machinery by higher photosynthetic rates, reducing Ψs (osmotic leaf potential), maintenance of chloroplast ultrastructure, and reduced ROS even under salinity. | Maintaining high levels of photosynthetic pigments, elevated parameters of photochemical efficiency (Fv/Fm), and regular phosphoenolpyruvate carboxylase activity recovered; (ii) preserving the chloroplast ultrastructure by decreasing both endogenous $H_2O_2$ and $\bullet O2^-$ contents; and (iii) regulate metabolites to the reestablishment of osmotic homeostasis and the scavenging of ROS. | Foliar $H_2O_2$ priming | Araújo et al. (2021) |
| *Triticum aestivum* | 100 μM/6 h | A positive effect on the growth, increasing the level of thiobarbituric acid reactive substances, stomal index, stomatal conductance and root dry weight, and reducing shoot dry weight. | Stimulating the SOD activity against salt stress. | Seed priming by $H_2O_2$ | Arican and Demirbas (2022) |
| *Ficus deltoidea* | 16 and 30 mM/once a week | Increased growth, accumulation of mineral (arsenic, iron, calcium, and potassium), stimulation of bioactive compounds (total phenolic, flavonoid content, vitexin, and isovitexin content), increased the leaf chlorophyll content, net photosynthetic rate, stomatal conductance, and quantum yield. | Increased stomatal opening and accumulated photosynthetic pigments. Produce a vigorous root system to increase the level of absorption area. | Foliar $H_2O_2$ priming | Nurnaeimah et al. (2020) |

(Continues)

**TABLE 2** (Continued)

| Plant | Concentrations of $H_2O_2$/duration of treatment | Positive effects | Mechanisms | Type of priming | Reference |
|---|---|---|---|---|---|
| *Helianthus annuus* | 1 mM with one application | An increase of 12% in the dry masses of leaves, 31% in the dry masses of stem, 33% in the dry masses of root, 23% in the total dry mass, 39% in the contents of Chl a, and 33% in the Chl a + b.<br>An increase of 53% and 20% in the water saturation deficit, 39% and 63% in the water content at saturation, 30% and 28% in the leaf succulence, 53% in the sclerophylly index.<br>An increase in the levels of soluble carbohydrates and free proline.<br>An increase in the APX activity of leaves and roots on an average 2.2- and 2.3-fold, respectively.<br>An increase of 9% in the CAT activity. | The balance of ion homeostasis (by reducing the levels of $Na^+$ and $Cl^-$ and increasing the levels of $K^+$) and homeostasis redox (due to increased antioxidant activity, mainly CAT). | Foliar $H_2O_2$ priming | Silva et al. (2020) |
| *Triticum aestivum* | 1 mM/8 h | Improvement of plant growth parameters, physiological parameters (CAT, peroxidase, and APX), pigments content, proline level, and mineral uptake ($K^+$, $Ca^{2+}$, and $Mg^{2+}$). | Energizing the cell division and formation of the secondary cell wall, increasing the antioxidant capacity of the cell, preventing the chlorophyll catabolism and increasing the activity of the antioxidant system. | Seed priming by $H_2O_2$ | Abdel Latef et al. (2019) |
| *Ocimum basilicum* | 1 μM/48 h | Increase in essential oil content, yield, productivity, and leaf succulence. | Improving the content of organic solutes plants, water uptake, dilution of $Na^+$ and $Cl^-$, and consequently, reduction of the toxic effects of these ions. | Foliar $H_2O_2$ priming | H. Silva et al. (2019) |
| *Pistacia vera* | 1 mM /24 h | Improvement of growth and reduction of total ascorbic acid and carotenoid and strong induction of APX and CAT activities.<br>A decrease in the MDA content and a decrease in the GSH (reduced glutathione) content. | Osmotic adjustment through enhancing activities of antioxidant enzymes or non-enzymatic antioxidant contents. | Foliar $H_2O_2$ priming | Bagheri et al. (2019) |
| *Cucumis sativus* | 1.5 mM/8 h | Increase in the activities of antioxidative enzymes such as manganese SOD, GPX, CAT, guaiacol peroxidase, APX, glutathione reductase, monodehydroascorbate reductase, dehydroascorbate reductase, and the antioxidants ascorbate and reduced glutathione.<br>Reducing the accumulation of $O2\bullet^-$ and $H_2O_2$. | Increasing antioxidant activity and decreasing lipid peroxidation to some extent, and thereby protecting the ultrastructure of most membranes (chloroplasts and mitochondria). | Foliar $H_2O_2$ priming | Z. J. Liu et al. (2010) |

(Continues)

**TABLE 2** (Continued)

| Plant | Concentrations of $H_2O_2$/duration of treatment | Positive effects | Mechanisms | Type of priming | Reference |
|---|---|---|---|---|---|
| *Allium cepa* | 1 mM/8 h | The increase in plant growth, productivity and water use efficiency, accumulation of compatible-solutes (polyols, sugars, and proline). | Improving the photosynthetic efficiency and plant water status by relative water content and membrane stability index. | Foliar $H_2O_2$ priming | Semida (2016) |
| *Oryza sativa* | 1–10 mM/12 h | Increase in the activity of APX, CAT, POD, SOD, and glucose-6-phosphate dehydrogenase in a concentration-dependent manner. | Enhancing the cellular antioxidant level. | Foliar $H_2O_2$ priming | X. Wang et al. (2013) |
| *Brassica napus* | 20 mM/12 h | Improving growth, increasing soluble sugars, reducing starch, changing $Na^+$ distribution in shoots, increasing phenolic accumulations, and stimulating the antioxidant defense systems (SOD, CAT, and POD). | Modulating the antioxidative mechanism involved in removing ROS and maintaining the cell membranes integrity. | Seed priming by $H_2O_2$ | Karimi et al. (2020) |

Abbreviations: AsA, ascorbate; APX, ascorbate peroxidase; CAT, catalase; GPX, glutathione peroxidases; GSH, glutathione; MDA, malondialdehyde; POD, peroxidase; ROS, reactive oxygen species; SOD, superoxide dismutase.

biosynthesis in obtaining plants resistant to pathogens, metallic stress, and also salinity stress has been reported (Chun et al., 2018; Gangopadhyay et al., 2016; Kopyra et al., 2003; Mhlongo et al., 2014; Paulert et al., 2010). For example, Khairy et al.'s (2016) in vitro study showed that the application of NO as a priming agent to tobacco plants cultured in vitro in the presence of cadmium or copper ameliorated growth by elevating rubisco and rubisco activase activity in comparison with plants treated with toxic metals without nitric oxide pretreatment.

Although reports evaluating the effects of typical priming in in vitro culture are still scarce due to the novelty of this concept, the aforementioned findings may be used to improve our knowledge of $H_2O_2$ priming–salinity interaction in vitro for possible exploitation in plant science and related technologies. However, it should be emphasized that convincing evidence of this interaction is rare, and further studies are needed to figure out the potential benefits of in vitro priming ($H_2O_2$) technology in plant science.

# 4 | CHALLENGES AND DISADVANTAGES

While the present review highlights the potential benefits of $H_2O_2$ priming as an economical non-expensive and easy-to-handle way, there is still a significant gap between research

on $H_2O_2$ priming and its practical application in agriculture. Therefore, addressing the challenges and barriers that hinder its widespread implementation would provide a more comprehensive perspective. Some of these challenges are mentioned below.

According to the published articles, priming can be used in different growth stages of the plant life cycle and in different parts of the plant, but in the case of hydrogen peroxide, the reports are related to seeds (often) and the foliar parts of plants (rarely). The reason for more use of seeds is probably the simplicity of implementing this technique in terms of laboratory facilities, experts, and operational costs. However, several challenges could be highlighted for seed priming. After priming, the seeds are redried to their original moisture content to allow the storage of the primed seeds, or they can be sown directly. The primary disadvantage observed with primed seeds is that the rapid redrying process can reduce the longevity of the seeds, so the storage life of primed seeds can be shorter than that of unprimed seeds. Priming may also result in the loss of seed desiccation tolerance, and there may be inconsistencies in germination performance. However, the optimization of the seed priming process is necessary especially at the commercial scale, due to several factors that can affect the seed response to primers, such as the concentration of the priming solution, the osmotic or matric potential, the duration of priming, temperature, seed vigor, plant species, storage condition, and the extent of aeration. Examples
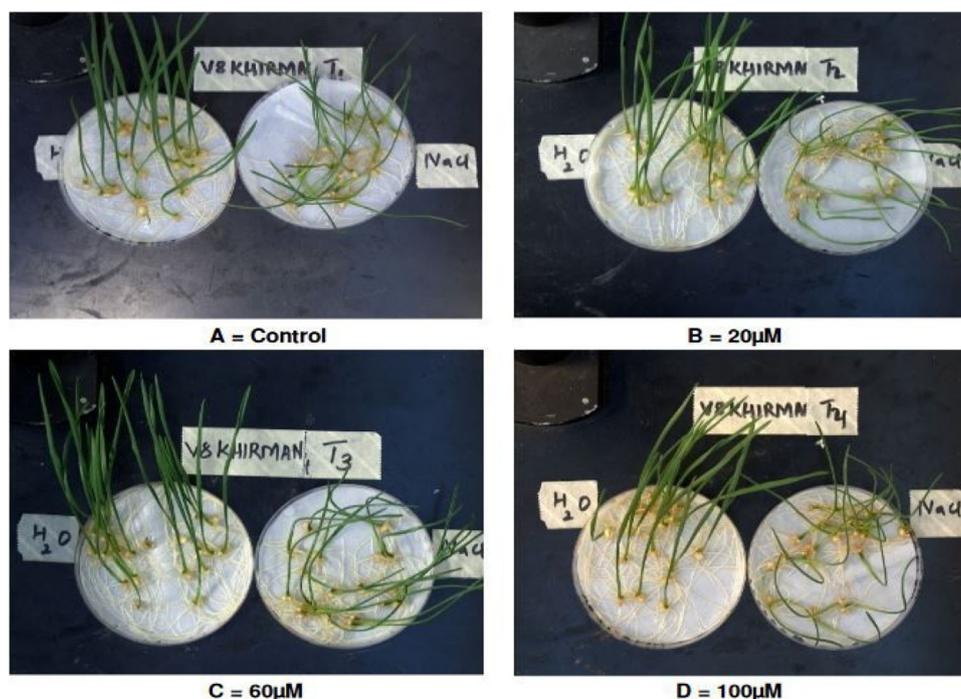
**FIGURE 3** Germination under the influence of genotypes, salinity levels, and $H_2O_2$ treatment on wheat genotypes. Different $H_2O_2$ concentrations significantly influenced the germination percentage, which improved with the increasing concentration of hydrogen peroxide both in water and NaCl treatments irrespective of cultivars (taken from Panhwar et al., 2021).
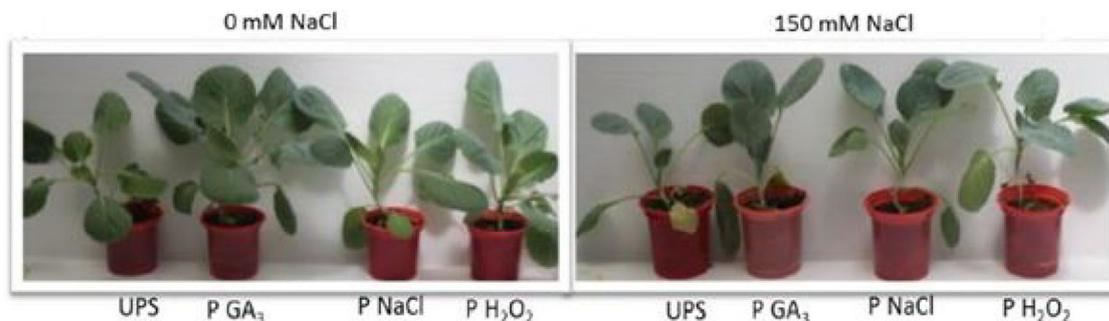


**FIGURE 4** The impact of three seed priming agents; $H_2O_2$, gibberellic acid, and NaCl on the oxidative stress status in primed seed (P) and un-primed seed (UPS) germination dynamics and growth establishment of cauliflower seedlings subsequently grown under salt stress. These findings support the hypothesis that cauliflower plants, when exposed to salt stress benefit from $H_2O_2$ seed priming, as a pre-germination stimulus, to prevent itself from subsequent oxidative injuries (salt stress) (taken from Ellouzi et al., 2021).

illustrating the impact of the concentration of the priming solution ($H_2O_2$) and various priming agents on seed germination are depicted in Figures 3 and 4, respectively.

Based on the mentioned points, the following questions are still open: Is it better to use seed or seedling priming for specific stress/species? What is the economic way with the best potential for priming plants with $H_2O_2$ especially at a commercial scale and under field conditions? Among the following methods of $H_2O_2$ priming, which one yields the best results, seed or seedling priming, priming by $H_2O_2$ to the soil or in the hydroponics solution, or priming by spraying foliar? The ways regarding hydrogen peroxide priming have

not been investigated so far. Moreover, little information has been reported on the seedling development of plants subsequent to seed priming at the commercial scale and under field conditions.

On the other hand, the role of different parts of plants priming varies with plant species, and it generally depends on the type of primer and also the nature of applied stress. Hence, determining whether $H_2O_2$ priming may protect plants from oxidative stress often induced by salinity in the multiple priming methods or various biotic or abiotic stresses at the same time deserves attention. However, the effects of $H_2O_2$ priming in multiple priming/stresses conditions on

antioxidant machinery, growth, development, and so on, of the salt-stressed plants are still unclear.

However, several other fundamental questions still remain, which according to our comprehensive review, no scientific reports have been published in these fields. For example, can the beneficial effects of $H_2O_2$ application only be observed in plants under salinity stress? Can the signals generated in the primed tissues also be transferred to the next generations? Could plants grown from primed tissues use these early signals for a better reaction during growth under salt stress conditions? Do the beneficial effects of $H_2O_2$ application occur in all plants and for all types of stresses? In which plnants do these effective signals end with the end of the salinity stress? What happens with recurrent stresses? Can $H_2O_2$ priming cause significant negative reactions? In addition, the effectiveness of factors such as cost, scalability, and potential limitations in different agricultural systems have not yet been evaluated by researchers.

# 5 | CONCLUDING REMARKS AND FUTURE PERSPECTIVES

In conclusion, as described in this review, $H_2O_2$ pre-priming of seeds, seedlings, or other parts of plants as an inferential signal that aids in protecting plants against salinity stress has important features: it is easily applied to numerous plants, is not labor-consuming, does not require complex laboratory equipment, and is relatively inexpensive. For these reasons, $H_2O_2$ priming can be routinely considered a promising candidate in agricultural (conventional and modern) and horticultural practice worldwide. These are inevitable advantages over the induction of stress tolerance through modern genetic engineering techniques, and thus new and improved $H_2O_2$ priming methods are expected to be continuously developed. Therefore, the collective knowledge gathered here, covering various aspects of the $H_2O_2$ priming phenomenon, may facilitate the design and conduct of future research on plant tolerance to salinity or other abiotic stresses. However, future research needs to focus on several issues: elucidating how priming can be applied on a large scale to diverse plants, understanding biochemical and molecular mechanisms of $H_2O_2$ priming for precise and reliable applications of this approach, understanding specific roles of $H_2O_2$ signaling under stressed/non-stressed conditions in the conflict between crops/plants and ecological variables for advancing sustainable farming, investigating the evolutionary and ecological function of priming, and figuring out the potential benefits of in vitro priming ($H_2O_2$) technology in plant science.

## AUTHOR CONTRIBUTIONS
**Kiarash Jamshidi Goharrizi**: Conceptualization; investigation; project administration; writing—review and editing. **Soraya Karami**: Conceptualization; investigation; project administration; writing—review and editing. **Sedighe Ghanaei**: Investigation; writing—original draft.

## CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

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