

REVIEW

Crop Ecology and Physiology

Exploring the role of exogenous salicylic acid in cereals resilience to water deficit stress: Advances and challenges

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Abstract

Salicylic acid (SA) is an elicitor of abiotic stress tolerance in plants, but a comparative analysis of its effects across cereals remains under-explored. This review article assesses the literature on the biological functioning of exogenous SA application (foliar- or root-applied) in water-stressed cereals. Research has examined exogenous SA applications as a strategy of growth improvement in water-deficient environments mainly in wheat (*Triticum* spp.), maize (*Zea mays* L.), and rice (*Oryza sativa* L.), as well as barley (*Hordeum vulgare* L.). Exogenous SA applications in water-deficient environments were examined in the literature mostly as foliar applications at a variety of application rates, with 0.50–2.0 mM appearing more often across all cereals. Among cereals, SA rates ranged from 0.50 to 1.50 mM in wheat and maize (85% and 86% of the studies, respectively), from 0.25 to 0.70 mM in rice (83% of the studies), and in the area of 0.50 mM in barley. Except for one study on wheat and one study on maize, the remaining studies noted that exogenous SA promoted cereal growth in water-stressed environments in terms of biomass production. Improvement of cereal growth with exogenous SA was associated with (i) boosting the production of osmolytes, thus preserving water in plants, (ii) improving the enzymatic activity of antioxidant enzymes, thus maintaining intracellular redox homeostasis, and (iii) protecting chlorophyll, thus maintaining the photosynthetic capacity of water-stressed plants. Bridging the gap between studies under controlled conditions and field applications is necessary for developing on-farm applications as practical agronomic methods that will increase cereal production in a changing climate.

Plain Language Summary

This review article assesses the literature on the biological functioning of exogenous salicylic acid application in water-stressed cereals. Research has examined exogenous salicylic acid as a strategy to improve growth in water-deficient environments, mainly

Abbreviations: ABA, abscisic acid; HM, heavy metal; JA, jasmonic acid; ROS, reactive oxygen species; SA, salicylic acid.

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in wheat, maize, and rice, as well as barley. Most studies examined exogenous salicylic acid in water stress conditions as foliar applications at a variety of application rates, with 0.50–2.0 mM being the most common across all cereals. Except for one study on wheat and one on maize, all other studies noted that exogenous salicylic acid promoted the growth of cereals in water-stressed environments in terms of biomass production. Despite its promise as a tool to boost cereal resilience to water deficit stress, the optimal salicylic acid concentration, along with the frequency and timing of exogenous SA applications for effective defense of cereals in water-deficient environments, should be defined.

1 | INTRODUCTION

Cereals are fundamental crops for the human diet and animal nutrition globally. Therefore, food security is significantly impacted by cereal production security worldwide (Goff & Salmeron, 2004). Cereals are susceptible to environmental stresses, most notably during the reproductive stage (Daryanto et al., 2017). For example, water availability and temperature often determine grain yield, in addition to agronomic practices. Water deficit stress restricts cereal productivity, mostly in the arid and semi-arid tropics, where lack of water, especially during the grain filling, causes serious yield losses. Thus, grain production in water-deficient environments is a difficult task (Fathi & Tari, 2016). From an agronomic point of view, we can define drought as a lengthy period with insufficient rainfall, which subsequently reduces soil water through evaporation or transpiration, rendering it insufficient for crop needs (Kebede et al., 2019). According to Ogbaga et al. (2020), water deficit stress can refer to irrigation restrictions imposed through experimental treatments resembling drought conditions. The terms “drought stress” and “water deficit stress” are used interchangeably, as both describe water limitation during experiments (Ogbaga et al., 2020). In the current review article, the term “water deficit stress” is used throughout the text to prevent misunderstanding and confusion. Water deficit stress will threaten grain productivity, a challenge that is made worse by the effects of climate instability and the depletion of water supplies (Haghpanah et al., 2024).

Water deficit stress severely affects plant growth and development, leading to critical consequences, such as dehydration stress, loss of cellular turgor, disruption of membranes, inhibition of metabolite production, depletion of cellular energy, nutritional imbalance, reduced photosynthetic efficiency, and oxidative stress (Haghpanah et al., 2024; Seleiman et al., 2021). Yet, the magnitude of crop injury caused by water deficit events is rather unpredictable, as vegetation conditions, precipitation, soil water-holding capacity, and evapotranspiration are involved. Water deficit stress influences plant

growth by impairing water relations, nutrient absorption, photosynthetic rate, and distribution of assimilates, which all contribute to serious yield decline (Farooq, Wahid, et al., 2009; Praba et al., 2009). Tolerant cultivars, plant hormones, mineral nutrients, and friendly microbes can promote crop productivity in water-deficient environments, given that such strategies can increase crop productivity in stressful environments (H. Kaur, Kohli, et al., 2021). However, the production of cultivars that are tolerant to water deficit stress remains a challenging task due to the complexity arising from the quantitative inheritance of resilience to water deficit stress, which involves the interaction of polygenes in multiple pathways rather than the presence of a few major genes (Haghpanah et al., 2024; Kebede et al., 2019).

Phytohormones, such as abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA), and ethylene, are essential in controlling the reaction of plants to abiotic stressors (B. Ahmad et al., 2019; Iqbal et al., 2022; Jogawat et al., 2021). In cereals, such substances can be useful tools for modulating growth regulation, for example, by improving metabolic activity and enhancing yield under abiotic stresses, thereby supporting sustainable farming practices (Kosakivska et al., 2022; Voytenko & Kosakivska, 2025). Exogenous application of different phytohormones, such as ABA, melatonin, SA, and JA, has been tested to increase resistance to water deficit stress in wheat (A. Ahmad, Aslam, et al., 2021; Javadipour et al., 2022; M. Kaur et al., 2014; J. Li, Li, et al., 2024), barley (Abdelaal et al., 2020; Habibi, 2012), maize (Al Rawi et al., 2021; Guo et al., 2020; Jiang et al., 2022; Y. F. Wang et al., 2021), and rice (Farooq, Basra, et al., 2009; Z. Khan et al., 2024; Sohag et al., 2020; Teng et al., 2014). Among these, SA has been observed to significantly ease the impact of water deficit stress on plants by regulating gene expression caused by water deficit stress, protecting cells through elevated antioxidant activity, and improving water-use efficiency (Arpita et al., 2024; W. Song et al., 2023). Furthermore, exogenous SA has been used to improve resilience to salinity stress in wheat (Z. Ahmad, Waraich, et al., 2021; El-Hawary et al., 2023), barley (Hanif et al., 2024; Tabur et al., 2021),

rice (Jini & Joseph, 2017; Pai & Sharma, 2023), and maize (Al-Alawy & Al-Samerria, 2021; Granaz et al., 2022), as well as sunflower (A. Liu et al., 2024), French beans (Youssef et al., 2023), faba beans (Dawood et al., 2022; El-Beltagi et al., 2025), and alfalfa (Horchani et al., 2023). Lastly, SA can be essential for shielding plants against the adverse impact of heavy metal (HM) stress, by alleviating HM toxicity in plant organs (Amjadi et al., 2021; Jiang et al., 2022; Kanwal et al., 2025; Nizar et al., 2022; Tang et al., 2024; Zaid et al., 2020; Zaid et al., 2022). Therefore, supplemental use of SA is examined for its capacity to support crop production under stressful conditions. Nevertheless, crops vary greatly in their tolerance to abiotic stresses, while high SA rates might even be harmful to plant growth.

SA is an elicitor of abiotic stress tolerance in plants, but there is a gap in the literature pertaining to a comparison of the outcomes of its exogenous use (foliar- or root-applied) across various cereals. The goal of the present review article is to outline the peer-reviewed literature on the biological impact of exogenous SA application (foliar- or root-applied) on water-stressed cereals, highlighting inconsistencies across studies and potential contrasting responses between cereals. The findings will improve comprehension of the effects of exogenous SA application on cereals and thus optimize the use of exogenous SA in cereals. By revealing factors influencing the efficiency of exogenous SA application on major crops, we could enhance plant performance in stressful environments and promote the sustainability of produce. This review article evaluates the existing evidence in the peer-reviewed literature on whether exogenous SA application can improve the growth of water-stressed cereals. To better frame the literature synthesis, we set the following research questions, as illustrated in Figure 1: (i) What are the most common application methods and rates of exogenous SA for improving growth of cereals in water-deficient environments? (ii) Are there inconsistencies across studies in terms of cereal's response to the exogenous SA application? (iii) What are the major effects

Core Ideas

- The biological functioning of exogenous salicylic acid (SA) applications (foliar- or root-applied) in water-stressed cereals is reviewed.
- Research has examined exogenous SA applications as a strategy to improve growth in water-deficient environments, mainly in wheat, maize, and rice.
- Research has examined exogenous SA supply mostly as foliar applications at a variety of rates, with rates ranging from 0.50 to 2.0 mM appearing more often.
- SA rates ranged from 0.50 to 1.50 mM in wheat and maize (85% and 86% of the studies, respectively) and from 0.25 to 0.70 mM in rice (83% of the studies).
- The optimal SA concentration, along with the frequency and timing of SA applications for the defense of cereals in water-deficient environments, should be defined.

of the exogenous SA application on growth of water-stressed cereals, and which are the main mechanisms involved? (iv) Do cereal species exhibit contrasting responses to exogenous SA application? (v) What are the potential practical applications of the findings in cereal cultivation? and (vi) Which knowledge gaps are revealed based on the above analysis, and how should they be addressed to advance the efficiency of foliar-applied SA in water-stressed cereals?

By focusing on cereal crops, defining clear research questions, and uncovering the benefits and pitfalls of SA use to mitigate water stress, the current review differs substantially in focus from recent excellent reviews (Altaf et al., 2023; Chen et al., 2023; Elsisli et al., 2024; Yang et al., 2023), which



FIGURE 1 Research questions set in this review article to better frame the literature synthesis. SA, salicylic acid.

primarily concentrated on horticultural crops grown under various abiotic stresses. Bearing that in mind, the present review is a unique attempt to connect cereal physiological responses to water stress with the potential use of SA as a practical means of enhancing drought tolerance. Ultimately, the connection between cereal physiological responses and the potential use of SA as a practical agronomic tool provides a critical foundation that will guide future breeding strategies and effective crop management programs for enhancing drought tolerance in a changing climate.

2 | LITERATURE IDENTIFICATION

The article was based on English-language peer-reviewed publications identified in the Scopus database without a time limit. We applied a criteria-based assessment of coverage to ensure that relevant studies are included, according to the literature (Meline, 2015). In this context, we used the following keywords for the literature search: (i) “salicylic acid” AND “drought stress,” (ii) “salicylic acid” AND “water stress,” and (iii) “salicylic acid” AND “water deficit.” The initial search yielded 252 publications. Based on the research question(s) set for this review article, eligible publications for inclusion in the analysis were those reporting exogenous SA application (foliar- or root-applied) in cereals under conditions of any kind of water deficit stress occurring at any time of the plant ontogenic cycle. On the other hand, non-eligible publications were those publications in the Scopus database that were related to specific forms of SA (e.g., nanoparticles), specific application methods of SA (e.g., seed treatment), the effects of SA combined with other agents (minerals or other phytohormones), or the effects of water deficit stress combined with other abiotic stresses. According to the above criteria, 55 publications were eligible for inclusion and evaluation. The rationale for the exclusion criteria was to (i) facilitate comparisons of the SA effects among studies, (ii) minimize the risk of ambiguity in interpretation, and (iii) better serve the objective of this review. For example, including cases referring to SA application via seed priming, in combination with other agents, or on cereal plants exposed to combined stresses, which we finally excluded from this work, would complicate comparisons of SA effects across studies and add uncertainty to the evaluation of heterogeneous cases. Furthermore, establishing clear exclusion criteria is a simple way to better serve the objective of this work, namely, to facilitate comprehension of the physiological effects of SA application on growth of water-stressed cereals. We recognize, however, that some excluded cases are potentially relevant to real-field scenarios, because in reality crops experience combined stresses under field conditions. From this perspective, we acknowledge the exclusion of potentially relevant cases as a limitation of this work, which might narrow the applicability of the findings to

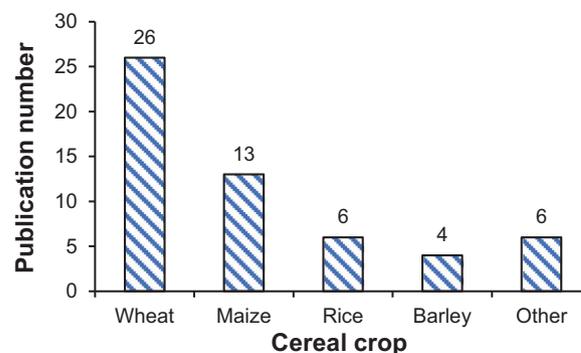


FIGURE 2 The selected studies referring to the effect of salicylic acid (SA) on water-stressed cereal species.

a certain extent. Of the relevant studies identified in the literature (55 publications), 26 referred to wheat (*Triticum* spp.), 13 referred to maize (*Zea mays* L.), six referred to rice (*Oryza sativa* L.), four referred to barley (*Hordeum vulgare* L.), and six referred to other cereals (Figure 2).

3 | LITERATURE ANALYSIS AND EMERGING TRENDS

3.1 | Wheat

The peer-reviewed literature on the biological impact of exogenous SA application on wheat in water-deficient environments is summarized in Table 1.

SA application on wheat grown in water-deficient environments included 26 studies published between 2003 and 2024 (Table 1). The SA application rates in water-stressed wheat ranged from 0.04 to 100 mM, with most cases falling between 0.50 and 1.50 mM.

SA foliar sprays maintained or improved the moisture content, dry biomass, and total chlorophyll of water-stressed wheat seedlings compared to control (non-sprayed) seedlings (B. Singh & Usha, 2003). Moreover, SA sprays, especially at the concentration of 3 mM, improved the nitrogen and protein content of water-stressed wheat leaves compared to seedlings under sufficient water (B. Singh & Usha, 2003). SA supply (0.036 and 0.072 mM) through nutrient solution improved wheat growth under non-stress conditions but did not show any beneficial effect under water deficiency, though one wheat cultivar performed better with lack of water (Waseem et al., 2006). Wheat plants that received 0.50 mM SA hydroponically did not tolerate water deficit stress, although they showed high activity of peroxidases (Horváth et al., 2007). Foliar-applied SA decreased water loss and the intensity of lipid peroxidation in water-stressed wheat plants, while it increased ethylene synthesis, peroxidase, catalase, and superoxide dismutase activity (Mamenko

TABLE 1 Selected studies referring to the effect of exogenous salicylic acid (SA) application on water-stressed wheat. SA rates are expressed in molar concentration units (mM), after conversion from the original source, to facilitate comparisons.

| No. | Cereal | SA rate (mM) | Reference |
|-----|--------|---------------|--|
| 1 | Wheat | 1.0, 2.0, 3.0 | Singh and Usha (2003) |
| 2 | Wheat | 0.036, 0.072 | Waseem et al. (2006) |
| 3 | Wheat | 0.50 | Horváth et al. (2007) |
| 4 | Wheat | – | Mamenko and Yaroshenko (2009) |
| 5 | Wheat | 0.50 | Loutfy et al. (2012) |
| 6 | Wheat | 0.50 | G. Kang et al. (2012) |
| 7 | Wheat | 0.50 | G. Z. Kang et al. (2013) |
| 8 | Wheat | 0.70 | Sharafizad et al. (2013) |
| 9 | Wheat | 0.10 | Abbasi et al. (2015) |
| 10 | Wheat | 1.0 | Arpali et al. (2016) |
| 11 | Wheat | 0.50 | Yavas and Unay (2016) |
| 12 | Wheat | 1.45 | Noreen et al. (2017) |
| 13 | Wheat | 0.50 | M. Sharma et al. (2017) |
| 14 | Wheat | 1.0 | Maghsoudi et al. (2018) |
| 15 | Wheat | 1.45 | Hafez and Farig (2019) |
| 16 | Wheat | 1.44 | Kareem et al. (2019) |
| 17 | Wheat | 1.0 | Maghsoudi et al. (2019) |
| 18 | Wheat | 1.0 | Sedaghat et al. (2020) |
| 19 | Wheat | 100 | A. Ahmad, Aslam et al. (2021) |
| 20 | Wheat | 1.0 | Shemi, Wang, Gheith, Hussain, Cholidah et al. (2021) |
| 21 | Wheat | 0.50 | Khalvandi et al. (2021) |
| 22 | Wheat | 0.70, 1.44 | M. I. R. Khan, Poor et al. (2022) |
| 23 | Wheat | 0.70 | Munsif et al. (2022) |
| 24 | Wheat | 1.0 | Sedaghat et al. (2022) |
| 25 | Wheat | 0.25, 0.50 | Sapakhova et al. (2022) |
| 26 | Wheat | 1.0 | Yadav et al. (2024) |

& Yaroshenko, 2009). Foliar-applied SA (0.50 mM) improved total biomass production in water-stressed wheat seedlings of cv Gemaza 1 (Figure 3a) and provoked soluble sugar accumulation (Figure 3b), while the enhanced tolerance to the lack of water with foliar-applied SA was attributed to solute accumulations, apart from proline biosynthesis (Loutfy et al., 2012).

Hydroponically administered SA (0.50 mM) promoted biomass production of water-stressed wheat plants and the improvement in biomass production was linked to proteins produced in the water-stressed plants (G. Kang et al., 2012). Similarly, hydroponically administered SA (0.50 mM) alleviated the impact of water deficit stress on the root growth and plant height of wheat (G. Z. Kang et al., 2013). Foliar SA application at 0.70 mM produced the maximum grain yield under water deficiency, whereas foliar SA application at 1.2 mM increased spike length and rate of grain growth but decreased grain yield and 1000-grain weight (Sharafizad et al., 2013).

SA supply (0.1 mM) administered via the nutrient solution provided some improvement in the antioxidant enzyme activity of water-stressed wheat plants, but the effect was inconsistent among enzymes and water deficiency levels (Abbasi et al., 2015). The above study reported that exogenous SA at any water deficit stress level inhibited lipid peroxidation. Foliar-applied SA (1.0 mM) increased the nutrient content in the flag leaf of wheat, although this effect differed according to the varieties (Arpali et al., 2016). Foliar SA application (0.50 mM) lowered the impact of low moisture on wheat cv Basribey plants by improving water status in the leaves (Figure 4a) under low moisture as well as promoting the antioxidant enzyme activity (Figure 4b) (Yavas & Unay, 2016).

Foliar SA application (1.45 mM) promoted the biological yield, chlorophyll content, and amino acid concentration of water-stressed wheat (Noreen et al., 2017). Foliar SA application at 0.50 mM increased the production of antioxidative enzymes, proline, and soluble sugars in two wheat cultivars

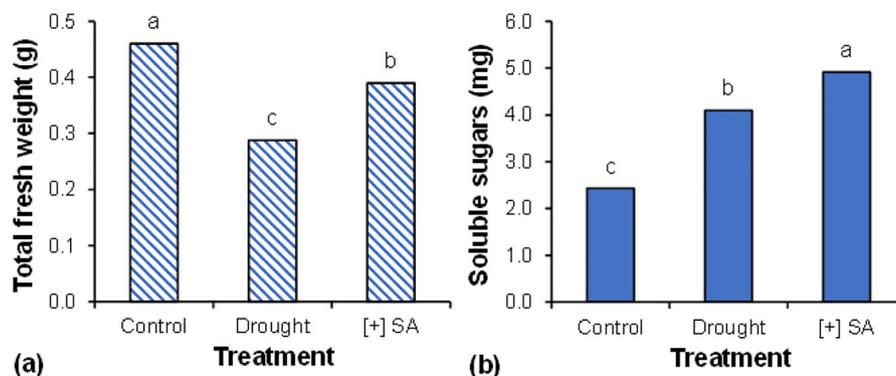


FIGURE 3 Impact of foliar application of salicylic acid (SA) (0.50 mM) on (a) total biomass production (g) and (b) soluble sugar production (mg) in water-stressed wheat seedlings of cv Gemaza 1 compared with the non-sprayed control. Values are means of three replications. Different letters denote significant differences among means according to the least significant difference test at $p < 0.05$. *Source:* Adapted from data of Loutfy et al. (2012).

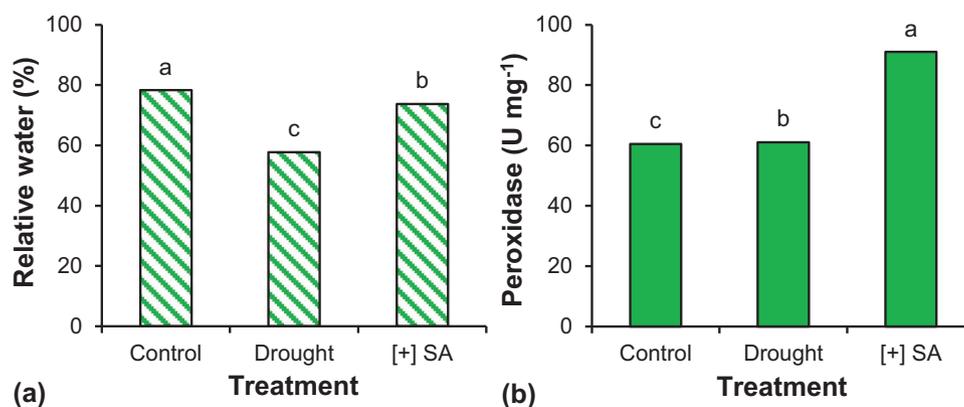


FIGURE 4 Impact of foliar application of salicylic acid (SA) (0.5 mM) on (a) relative water content (%) and (b) peroxidase activity (U mg⁻¹) in the leaves of water-stressed wheat seedlings of cv Basribey compared with the non-sprayed control. Values are means of three replications. Different letters denote significant differences among means according to the least significant difference test at $p < 0.05$. *Source:* Adapted from data of Yavas and Unay (2016).

grown with limited water (M. Sharma et al., 2017). Water deficit stress reduced leaf water and chlorophyll content in two wheat cultivars and caused electrolyte leakage in the leaves (Maghsoudi et al., 2018). In contrast, foliar-applied SA improved growth parameters and reduced electrolyte leakage in the leaves. Foliar-applied SA increased absorption of N, P, and K in water-stressed wheat plants as well as the relative water content and proline content, whereas it decreased Na uptake and stomatal conductance compared to the non-sprayed plants (Hafez & Farig, 2019). The above changes improved the number of spikes per m², the number of grains per spike, and the 1000-grain weight. Foliar SA application improved biomass production and yield components of wheat grown with limited water and stimulated expression of the *CBF14* gene (Kareem et al., 2019). Foliar SA application improved the water content in the leaves and grain yield of two water-stressed wheat cultivars (Maghsoudi et al.,

2019). In addition, foliar-applied SA promoted the activity of key antioxidant enzymes, increased the accumulation of osmolytes, and lowered the levels of H₂O₂ and malondialdehyde in water-stressed plants. Likewise, foliar-applied SA (1.0 mM) increased osmolyte production, stomatal conductance, and photosynthesis of wheat plants (Sedaghat et al., 2020). Foliar-applied SA (100 mM) improved the stability of membranes, maintained chlorophyll content, improved photosynthetic rates, promoted antioxidant capacity of wheat plants, and preserved water under low-moisture conditions (A. Ahmad, Aslam, et al., 2021). Foliar SA applications (1.0 mM) increased the activity of antioxidant enzymes and promoted proline production under water deficiency (Shemi, Wang, Gheith, Hussain, Cholidah, et al., 2021). Foliar SA application (0.50 mM) ameliorated the negative impact of low moisture on Sardari wheat ecotypes via improving photosynthesis, retaining membrane permeability, and

TABLE 2 Selected studies referring to the effect of exogenous salicylic acid (SA) application on water-stressed maize. SA rates are expressed in molar concentration units (mM), after conversion from the original source, to facilitate comparisons.

| No. | Cereal | SA rate (mM) | Reference |
|-----|--------|------------------|---|
| 1 | Maize | 0.50 | Németh et al. (2002) |
| 2 | Maize | 0.36, 0.72, 1.45 | Rao et al. (2012) |
| 3 | Maize | 0.001 | Saruhan et al. (2012) |
| 4 | Maize | 2.0 | W. Y. Song et al. (2014) |
| 5 | Maize | 0.01, 0.1 | Latif et al. (2016) |
| 6 | Maize | 0.50 | Maswada et al. (2017) |
| 7 | Maize | 0.01 | Shan and Wang (2017) |
| 8 | Maize | 0.02 | Quiroga et al. (2018) |
| 9 | Maize | 1.0 | Bijanazadeh et al. (2019) |
| 10 | Maize | 1.0 | Qasim et al. (2019) |
| 11 | Maize | 0.72, 1.45, 2.2 | Al Rawi et al. (2021) |
| 12 | Maize | 1.0 | Shemi, Wang, Gheith, Hussain, Hussain et al. (2021) |
| 13 | Maize | 0.01 | Somtrakoon and Chouychai (2022) |

promoting the activity of antioxidant enzymes (Khalvandi et al., 2021). Most of the genotypes had enhanced proline accumulation at both levels of SA (0.7 and 1.44 mM) in comparison with no spraying of SA. Osmotic potential was generally decreased in water deficit environments with SA spray (M. I. R. Khan, Poor, et al., 2022). Foliar SA application (0.7 mM) increased biomass, yield components, and grain yield, as well as the antioxidant system profile of wheat under both normal and low-moisture conditions (Mun-sif et al., 2022). Foliar SA application (1.0 mM) improved the performance of water-stressed wheat plants by increasing antioxidant enzyme activity and lowering the levels of hydrogen peroxide, which decreased the oxidation stress in different wheat cultivars (Sedaghat et al., 2022). Foliar SA application improved the activity of antioxidant enzymes in water-stressed wheat plants (Sapakhova et al., 2022). Foliar SA application (1.0 mM) increased grain yield and yield attributes of water-stressed wheat due to increased chlorophyll content and photosynthesis, increased intercellular CO₂ concentration, and stimulatory changes in other attributes (Yadav et al., 2024). Overall, in wheat, SA rates ranging from 0.50 to 1.50 mM consistently improved growth, biomass production, and antioxidant defense.

3.2 | Maize

The peer-reviewed literature on the biological impact of exogenous SA application on maize in water-deficient environments is summarized in Table 2.

SA application on maize grown in water-deficient environments included 13 studies published from 2002 until 2022 (Table 2). The SA application rates in water-stressed maize

ranged from 0.001 to 2.2 mM, although the majority of cases utilized rates from 0.50 to 1.50 mM.

SA supply (0.50 mM) through hydroponic solution increased putrescine content in young maize plants but decreased photosynthesis and conductivity of the stomata, causing sensitivity of maize plants to lack of water (Németh et al., 2002). Foliar SA application (0.72 mM) stabilized the leaf membranes, maintained chlorophyll, and improved the water status in maize under low moisture (Rao et al., 2012). Foliar-applied SA improved the activity of all antioxidant enzymes in maize plants under low moisture (Saruhan et al., 2012). Treatments with SA showed that this substance had some mitigating effects on the growth of maize seedlings under polyethylene glycol (PEG)-simulated water deficit stress (Song et al., 2014). Foliar-applied SA ameliorated the adverse effects of water deficit stress on root length and root area as well as leaf relative water content and total biomass production (Latif et al., 2016). Foliar SA application (0.50 mM) advanced plant height, biomass, leaf area, and relative growth rate of water-stressed maize plants (Maswada et al., 2017). In the same study, foliar SA application increased the concentration of photosynthetic pigments in maize plants under conditions of irrigation deficit through increasing water content and proline accumulation. Foliar-applied SA increased root hydraulic conductivity and leaf water status of maize in a water-stressed environment (Shan & Wang, 2017). Foliar-applied SA decreased hydraulic conductivity of the root, which was attributed to the regulation of root aquaporins (Quiroga et al., 2018). Similarly, water-stressed maize plants of the hybrid SC 705 that were treated with SA displayed higher levels of photosynthetic pigments, water content, and K⁺ (Bijanazadeh et al., 2019). Foliar-applied SA (0.50 mM) at the six-leaf stage of the maize hybrid DK 6789

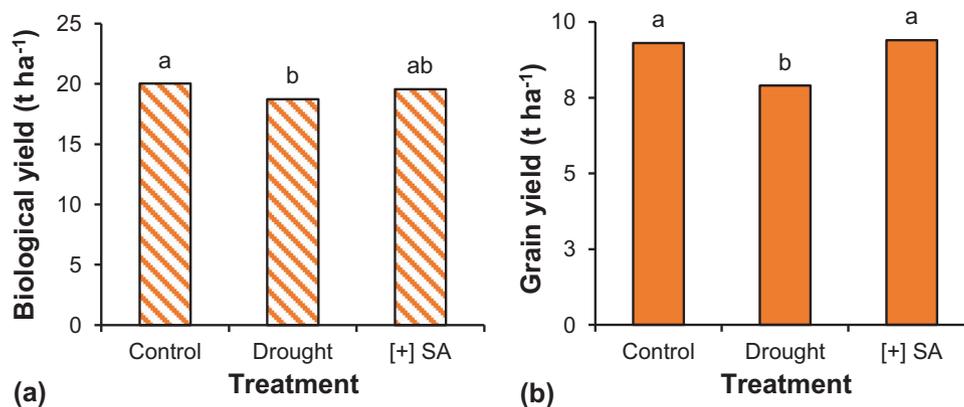


FIGURE 5 Impact of foliar application of salicylic acid (SA) (1.0 mM) on (a) biological yield (t ha^{-1}) and (b) grain yield (t ha^{-1}) of water-stressed maize hybrid DK 6789 compared with the non-sprayed control. Values are means of three replications. Different letters denote significant differences among means according to Tukey's honest significance difference test at $p < 0.05$. Source: Adapted from data of Qasim et al. (2019).

mitigated the harmful effects of water deficit stress, imposed at the initiation of the silking stage, by improving the biological yield (Figure 5a) and grain yield of water-stressed maize (Figure 5b) (Qasim et al., 2019).

Similarly, foliar SA application (0.72, 1.45, and 2.17 mM) increased the growth characteristics of water-stressed maize (Al Rawi et al., 2021). The same response was observed with foliar spraying of SA (1.0 mM), which improved water status, chlorophyll levels, and gas-exchange parameters of water-stressed maize plants compared with well water conditions (Shemi, Wang, Gheith, Hussain, Hussain, et al., 2021). In contrast, another study found that two foliar SA applications (0.01 mM) had no substantial effect on shoot growth, ear weight, or ear diameter of water-stressed maize, although it increased shoot fresh weight under normal irrigation (Somtrakoon & Chouychai, 2022). Overall, in maize, SA rates ranging from 0.50 to 1.50 mM consistently improved growth, biomass production, and antioxidant defense.

3.3 | Rice

The peer-reviewed literature on the biological impact of exogenous SA application on water-stressed rice is summarized in Table 3.

SA application on rice grown in water-deficient environments included six studies published between 2009 and 2023 (Table 3). The SA application rates in rice had an overall range from 0.25 to 1.10 mM, with most cases ranging from 0.25 to 0.70 mM.

SA supply (0.72 mM) improved rice growth irrespective of stress (Farooq, Basra, et al., 2009). Foliar SA supply preserved water and promoted metabolite production and carbon assimilation in water-stressed rice (Farooq et al., 2010). SA supply lowered oxidative damage in water-stressed rice by

increasing the activity of the antioxidant enzymes. SA supply also preserved photosynthetic pigments (Sohag et al., 2020). Foliar spray of SA increased the performance of water-stressed wheat plants in terms of dry weight production and nutritional status of the plants, and decreased the concentration of reactive oxygen species (ROS) (Asma et al., 2023). Foliar supply of SA at 0.25 mM improved growth parameters, promoted the activity of antioxidant enzymes, and enhanced metabolite accumulation in water-stressed rice cultivars (Kor-gaonker & Bhandari, 2023). The expression of the cytosolic ascorbate peroxidase gene, copper-zinc superoxide dismutase, and catalase gene *O_sCATA* was increased, compared to the 15% PEG 6000 treatment (Ubaidillah et al., 2023). Overall, in rice, SA rates ranging from 0.25 to 0.70 mM consistently improved growth parameters, biomass production, and antioxidant defense of plants.

3.4 | Barley

The peer-reviewed literature on the biological impact of exogenous SA application on barley grown in water-deficient environments is summarized in Table 4.

SA application on barley grown in water-deficient environments included four studies published from 2012 to 2023 (Table 4). The SA application rates in barley ranged from 0.05 to 1.50 mM, with most cases reporting the rate of 0.50 mM.

SA supply increased photosynthesis, net CO_2 assimilation, and dry weight rate in water-stressed barley plants (Habibi, 2012). SA supply (0.50 mM) improved aerial biomass, photosynthetic pigments, and K^+ in water-stressed barley leaves (Fayez & Bazaid, 2014). SA at 0.50 mM increased dry biomass, chlorophyll content, water availability, activity of antioxidant enzymes, and grain yield of water-stressed barley (Abdelaal et al., 2020). Foliar-applied SA stopped the

TABLE 3 Selected studies referring to the effect of exogenous salicylic acid (SA) application on water-stressed rice. SA rates are expressed in molar concentration units (mM), after conversion from the original source, to facilitate comparisons.

| No. | Cereal | SA rate (mM) | Reference |
|-----|--------|-----------------|--------------------------------|
| 1 | Rice | 0.36, 0.72, 1.1 | Farooq, Basra et al. (2009) |
| 2 | Rice | 0.72 | Farooq et al. (2010) |
| 3 | Rice | 0.50, 1.0 | Sohag et al. (2020) |
| 4 | Rice | 0.72 | Asma et al. (2023) |
| 5 | Rice | 0.25 | Korgaonker and Bhandari (2023) |
| 6 | Rice | 1.0 | Ubaidillah et al. (2023) |

TABLE 4 Selected studies referring to the effect of exogenous salicylic acid (SA) application on water-stressed barley. SA rates are expressed in molar concentration units (mM), after conversion from the original source, to facilitate comparisons.

| No. | Cereal | SA rate (mM) | Reference |
|-----|--------|----------------|-------------------------|
| 1 | Barley | 0.50 | Habibi (2012) |
| 2 | Barley | 0.05 | Fayez and Bazaid (2014) |
| 3 | Barley | 0.50 | Abdelal et al. (2020) |
| 4 | Barley | 0.50, 1.0, 1.5 | Islam et al. (2023) |

TABLE 5 Selected studies referring to the effect of exogenous salicylic acid (SA) application on other water-stressed cereals. SA rates are expressed in molar concentration units (mM), after conversion from the original source, to facilitate comparisons.

| No. | Cereal | SA rate (mM) | Reference |
|-----|--------------------|--------------|---------------------------|
| 1 | Oat | 0.1 | Canales et al. (2019) |
| 2 | Foxtail millet | 0.75, 1.5, 3 | Karimian et al. (2023) |
| 3 | Tall fescue | 1.0 | Pirnajmedin et al. (2020) |
| 4 | Tall fescue | 1.0 | Taleb et al. (2021) |
| 5 | Creeping bentgrass | 0.01 | Z. Li et al. (2017) |
| 6 | Perennial ryegrass | 0.25, 0.50 | Ma et al. (2020) |

buildup of ROS by promoting the activity of important antioxidant enzymes, including superoxide dismutase, ascorbate peroxidase, catalase, and glutathione peroxidase, thus limiting the levels of oxidative damage in the cells (Islam et al., 2023). Overall, in barley, the SA rate of 0.50 mM consistently improved growth parameters, biomass production, and antioxidant defense of plants.

3.5 | Other cereals

The peer-reviewed literature on the biological impact of exogenous SA application on other cereals grown in water-deficient environments is summarized in Table 5.

SA application on other cereals grown in water-deficient environments included six studies published from 2017 to 2023 (Table 5). The SA application rates in other cereals ranged from 0.01 to 3.0 mM, with most cases utilizing rates from 0.50 to 1.0 mM.

SA treatment reduced purescine levels in water-stressed oat (*Avena sativa* L.), while it increased those of spermine, which correlated with the down-regulation of the arginine decarboxylase gene and up-regulation of the S-adenosyl-methionine decarboxylase gene (Canales et al., 2019). Foliar spraying of 1.0 mM SA improved growth parameters of water-stressed foxtail millet (*Setaria italica* L.), including total chlorophyll content as well as fresh forage yield and seed yield (Karimian et al., 2023). Foliar SA application (1.0 mM) boosted water deficit tolerance and forage output in tall fescue (*Festuca arundinacea* Schreb.) by enhancing photosynthetic pigments and regulating both non-enzymatic and enzymatic antioxidant activity (Pirnajmedin et al., 2020). Foliar SA application (1.0 mM) improved root dry weight, root volume, and forage yield of water-stressed tall fescue plants compared to non-treated plants (Taleb et al., 2021). SA supply (0.01 mM) alleviated water deficit damage in creeping bentgrass (*Agrostis stolonifera* L.), for example, prevented electrolyte leakage and maintained water content in

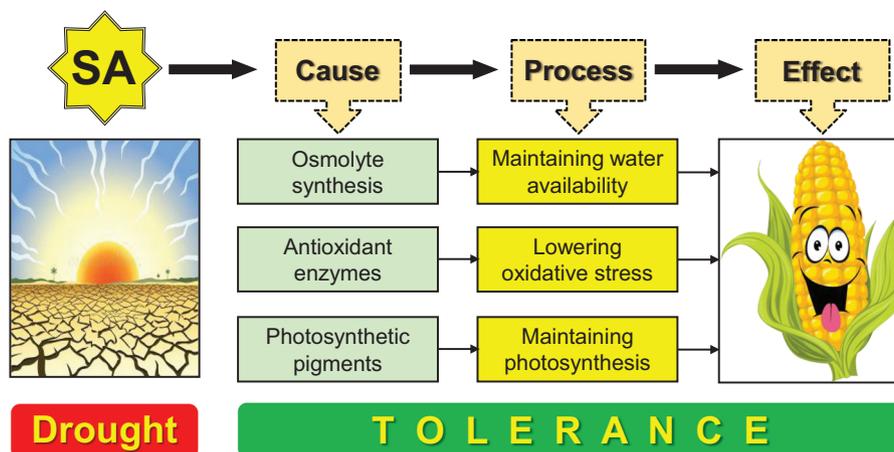


FIGURE 6 Major effects of exogenous salicylic acid (SA) on growth of water-stressed cereals.

the leaves (Z. Li et al., 2017). Foliar-applied SA increased the water status, chlorophyll levels, peroxidase and superoxide dismutase activity, along with proline and soluble sugars in water-stressed perennial ryegrass (*Lolium perenne* L.), while decreasing malondialdehyde content (Ma et al., 2020). Overall, in other cereals, SA rates ranging from 0.50 to 1.0 mM consistently improved growth parameters, biomass production, and antioxidant defense of plants.

4 | DISCUSSION

In this review article, we assessed the peer-reviewed literature on the biological functioning of exogenous SA application in cereals grown in water-deficient environments. Agronomically speaking, water deficit stress can relate to the timing of rainfall during the growing season or to abnormally low rainfall during that time (Passioura, 2012). However, to cover an adequate part of the academic literature and facilitate comprehension of the SA role as a stress alleviator in cereals, publications related to exogenous SA application on cereals under conditions of any kind of water deficit stress occurring at any time of the plant ontogenic cycle were selected. Except for one study on wheat and one study on maize, all the other studies noted that exogenous SA application enhanced growth parameters of cereals in water-limited environments in terms of biomass production, with application rates from 0.50 to 2.0 mM appearing more often across all cereals. Promotion of various physiological responses with exogenous SA accompanied improvement of growth parameters in the plants. In particular, SA was found to maintain water availability in plant tissues under water deficiency by promoting production of osmolytes, to promote the antioxidant capacity of plants, thus minimizing the harmful impact of oxidation by water deficit stress, and to protect the chlorophyll content of plants, thus supporting photosynthesis under water deficiency, as illustrated in Figure 6.

TABLE 6 Rate range for salicylic acid (SA) foliar application most frequently reported in water-stressed major cereals. All SA rates are expressed in molar concentration units (mM), after conversion from the original source, to facilitate comparisons.

| No. | Cereal | SA rate range (mM) |
|-----|-------------|--------------------|
| 1 | Wheat | 0.50–1.5 |
| 2 | Maize | 0.50–1.5 |
| 3 | Rice | 0.25–0.70 |
| 4 | Barley | 0.50 |
| 5 | All cereals | 0.50–2.0 |

4.1 | SA application methods and rates

Exogenous SA application in water-stressed cereals was examined in the literature mostly as foliar applications at a variety of application rates, with 0.50–2.0 mM appearing more often across all cereal species (Table 6). The majority of the studies across all cereals reported positive effects on growth of water-stressed cereals, with SA rates typically ranging from 0.50 to 1.50 mM in wheat and maize (85% and 86% of the studies, respectively), from 0.25 to 0.70 mM in rice (83% of the studies), and in the area of 0.50 mM in barley (Table 6). Due to the specific nature of each single study and the varying number of cases for each cereal, direct comparisons between cereals could be potentially invalid or misleading. Therefore, a substantial portion of the present review presents and discusses the results on a cereal-by-cereal basis for easy comprehension of the findings. However, as evident from Table 6, the published studies suggest a trend of higher SA application rates in water-stressed wheat and maize than in rice and barley.

The consistent enhancement of drought tolerance across cereal species, following SA application, can be attributed to the common physiological basis of growth and reproduction. Specific patterns that facilitate environmental adaptation

characterize this growth framework. Indeed, major cereals, such as wheat, maize, and rice, have evolved a high degree of adaptability, particularly in the timing of their life cycle, to align with seasonal changes. We can understand cereal yield formation in terms of crop growth (i.e., biomass production) and pattern of biomass allocation to the yield (Weiner et al., 2021). This process involves growth and differentiation in both vegetative and reproductive organs, which ultimately determines the total biomass produced and its subsequent distribution to the grains (Farooq et al., 2014). However, under stressful conditions such as water deficit, cereal growth is severely inhibited, leading to significant biomass reductions in wheat, maize, and rice (Perdomo et al., 2015). Furthermore, water stress strongly impacts flowering initiation and development, commonly resulting in abortive ovaries and infertile pollen (Qian et al., 2025).

No negative effects of SA application in water-deficit environments were reported in the reviewed literature. Even though the positive benefits of SA on stress tolerance are fairly well established, there are still questions regarding the optimal application method and concentration for alleviating water-deficit stress (Mohammed et al., 2023). The application method of SA can have a big impact on its effectiveness in enhancing plant growth under stressful conditions. Indeed, research across various plant species has demonstrated differential responses depending on the mode of SA application. In muskmelon (*Cucumis melo* L.), foliar SA application and seed soaking protected plants similarly against water deficit stress (Korkmaz et al., 2007). However, foliar SA application was better than seed soaking in promoting photosynthesis and plant growth of water-stressed rice (Farooq, Basra, et al., 2009). For tomato (*Solanum lycopersicon* L.) under salt stress, a combination of foliar and root SA pretreatment (before transplanting) was found to be the most efficient way of restoring plant growth (Souri & Tohidloo, 2019). In alfalfa (*Medicago sativa* L.), recent research noted that foliar application was more effective than root application of SA in mitigating the adverse effect of salinity on the growth and the biochemical characteristics of plants (Horchani et al., 2023). Similarly, SA application to the foliage or in combination with seed soaking were the best options for the optimal performance of wheat under different irrigation levels (Mohammed et al., 2023). Apart from cereals, foliar SA application is a useful tool for improving growth in diverse crops growing in water-deficit environments, including oilseeds, legumes, vegetables, medicinal plants, and certain ornamental and non-woody species (Damalas & Koutroubas, 2021).

4.2 | Inconsistencies across studies

The current scholarly literature reveals notable inconsistencies regarding the efficacy of SA application under water

deficiency. For example, no beneficial effect of root-applied SA (0.036 and 0.072 mM) on water-stressed wheat grown in 250-mL plastic beakers was observed, though one wheat cultivar displayed better tolerance to water deficit (Waseem et al., 2006). The lack of a beneficial effect of SA application on water-stressed wheat in this case might be related to the low SA rates (0.036 and 0.072 mM) examined in the study, as well as their administration through the root medium. The examined rates are the lowest among those used in water-stressed wheat, according to Table 1. Concerning the effective rate of SA for root application, studies reported inconsistent findings. For example, root-applied SA at 0.50–1.0 mM did not affect the growth of soybean seedlings, whereas a higher application rate of 5.0 mM had adverse effects on the seedling growth (Lian et al., 2000). Whatever the case, the ineffective SA rates (0.036 and 0.072 mM) tested in water-stressed wheat are clearly lower than those used in soybean. In light of the above evidence, the low SA rates could explain the neutral effect of SA on water-stressed wheat reported by Waseem et al. (2006). Similarly, in field-grown maize in water deficit conditions, two foliar SA applications (0.01 mM) did not improve shoot growth, ear weight, and ear diameter (Somtrakoon & Chouychai, 2022). The lack of beneficial effect of SA application on water-stressed maize in the above case might be related to the low SA rate (0.01 mM) examined in the study, combined with the late timing of application (20 and 50 days in a 60-day growth cycle), which probably limited SA absorption by maize leaves. The SA rate (0.01 mM) in this study ranks among the lowest SA rates used in water-stressed maize, according to Table 2. Furthermore, it is well known that leaf age affects leaf wettability and foliar absorption of solutes (Tie et al., 2023). In particular, plant age alters the chemical composition and microstructure of the leaf surface, which can restrict foliar absorption of solutes (Tie et al., 2023). Bearing the above information in mind, the low SA rates and the limited SA absorption by maize leaves could explain the neutral response of water-stressed maize to SA reported by Somtrakoon and Chouychai (2022). Apart from the above-mentioned explanations, the neutral effect of SA might also be related to species- or genotype-specific differences and to the intensity and duration of water deficit stress, which may alter the physiological response of plants to SA. These aspects should be tested in the future based on specifically predefined hypotheses.

4.3 | Major effects of exogenous SA application on cereals

4.3.1 | SA boosts the production of osmolytes

In the present review article, SA was found to maintain water availability in plant tissues under water deficiency by promot-

ing the production of osmolytes. Osmolytes are compounds that regulate the intracellular water levels as a plant reaction to the lack of water (Ozturk et al., 2021). Osmolyte accumulation contributes to the osmoprotection of cells, the maintenance of cell turgor, and the enhancement of soil water uptake in crop plants. Such compounds, which accumulate in the cytoplasm, can protect the metabolic machinery of cells from damage caused by dehydration. Furthermore, osmolyte accumulation decreases cellular osmotic potential, increasing the gradient for water flux and maintaining cell turgor. Therefore, as the soil dries, the osmolyte accumulation reduces plant water potential, enabling the plant to sustain water uptake from the soil.

Indeed, osmolyte production decreases osmotic potential and thus maintains water in cells, which sustains physiological processes in plants. Osmolytes regulate water absorption and maintain cell turgor without affecting plant metabolism (U. K. Ghosh et al., 2021). Research on exogenous application of osmolytes has shown that treated plants are better able to withstand environmental stressors compared with non-treated plants (Nahar et al., 2016; Rasheed et al., 2024). In particular, exogenous administration of single or combined osmolytes can have a significant role in enhancing drought resistance in many plant species.

However, field research on the relationship between osmolyte accumulation and crop yield has generally found no clear benefit (Sinclair & Rufty, 2022). This uncertainty appears to be mostly caused by failing to account for the temporary nature of soil water availability throughout the growth season, as there is no stable environment in which to assess the effect of osmolyte accumulation (Sinclair & Rufty, 2022). For this reason, several factors concerning foliar application of osmolytes under field conditions of water deficit should be considered. In particular, environmental factors can negatively affect uptake, making the yield advantage questionable. We recommend further research to clarify this issue.

SA has also been found to confer tolerance to water deficit stress in wheat by enhancing total soluble sugars (Loutfy et al., 2012). Indeed, the osmoregulatory processes of water-stressed plants also include increased concentrations of sugars (e.g., trehalose, sucrose, oligosaccharides, and fructans) as well as polyols (e.g., mannitol, sorbitol, and inositols) (Ozturk et al., 2021). In particular, the alleviation of water deficit stress by the accumulation of sugars takes place via the substitution of water molecules by the hydroxyl group of sugars. This substitution can replace water molecules and thus maintain hydrophilic interactions with cellular proteins and membranes, and it hampers the denaturation of proteins and membrane lipids through hydrogen bonding (H. Kaur, Manna, et al., 2021). Soluble sugar accumulation occurs after the breakdown of stored starch in source tissues, with sugars being transported to sink tissues to meet the

energy demands of plants and support other stress-responsive adaptive mechanisms (H. Kaur, Manna, et al., 2021).

Total soluble sugars are also involved in scavenging ROS in plants under stress (Saddhe et al., 2021). For example, by regenerating NADP⁺ in the chloroplast, proline synthesis stops the generation of ROS (La et al., 2019). Under water deficiency, SA promoted proline synthesis without affecting proline catabolism. This was evidenced by the upregulation of proline synthesis-related genes, while the expression of proline degradation-related genes remained unchanged, indicating that SA modulates the oxidized redox status caused by water deficit (La et al., 2019). In addition to their role in osmoprotection during stress, sugars also regulate gene expression in stressful environments (W. Song et al., 2023). Plants produce water-soluble carbohydrates in water-deficient environments, and the observed alterations in sugar metabolism may be a component of SA-induced stress tolerance (M. A. Khan, Shirazi, et al., 2022).

Undoubtedly, SA-regulated accumulation of different organic osmolytes promotes plant tolerance to abiotic stress due to maintenance of osmotic homeostasis. Water deficit stress impairs ionic balance, whereas K⁺, Na⁺, Cl⁻ and Ca²⁺ promote tolerance of plants to water deficit stress through ion homeostasis (Mukarram et al., 2021). K⁺/Cl⁻ ion homeostasis regulates stomata opening by affecting the function of the guard cells (Singh et al., 2015). Osmolytes may respond differently from species to species because different types of such molecules can be produced under stress conditions. Thus, additional information is required on the role of an osmolyte under stress with respect to other compounds produced in plant tissues.

4.3.2 | SA improves the antioxidant capacity and ROS scavenging

In the present review article, SA was found to promote the antioxidant capacity of cereals, thus minimizing the harmful impact of oxidative stress on plants. Oxidative stress generates ROS, which induces protein oxidation, lipid peroxidation, and DNA degradation (García-Caparrós et al., 2021). ROS are involved in different pathways of plant adjustment to abiotic stresses but are toxic secondary products of plant metabolism under stress (Mittler, 2002; Choudhury et al., 2017). ROS levels of a single cell can spread by cell-to-cell communication in an organism (Peláez-Vico et al., 2024). Injuries from ROS may eventually cause plant death.

The antioxidant system of plants protects cellular structures from oxidative damage and is of particular importance in mitigating the negative effects of water deficit stress on plants (Kolupaev et al., 2023). Almost every cellular compartment of plants has antioxidant enzymes and related substances, indicating the significance of ROS detoxification

for defense against a range of stressors (Mittler et al., 2004). The antioxidant system prevents ROS accumulation in the plant cells through the production of enzymatic and non-enzymatic antioxidants (García-Caparrós et al., 2021). Such antioxidant molecules can maintain the equilibrium between generation and degradation of ROS, whereas the equilibrium gets disturbed under stressful conditions, generating oxidative stress in the cells (Anjum et al., 2012; Gill & Tuteja, 2010; Nafees et al., 2019). ROS scavengers, essential molecules of the antioxidant machinery in the cells, regulate this sensitive balance, thus preventing cell damage under conditions of stress.

The main enzymatic antioxidants that are necessary for maintaining ROS homeostasis are ascorbate peroxidase, superoxide dismutase, catalase, and glutathione reductase. These enzymes function together as a complex system to minimize, buffer, and scavenge ROS efficiently (Rajput et al., 2021). Better knowledge of regulating ROS signaling is still required, despite the fact that genetic engineering techniques have significantly improved ROS scavenging in the production of stress-resilient crops (Mishra et al., 2023). Bolstering the natural antioxidant defense of plants and their ability to lessen the impact of oxidative stress could be a viable strategy for reducing oxidative stress levels in the field environment and increasing crop output and tolerance to water stress (Sun et al., 2024). However, one of the primary challenges is the variability in environmental conditions, which can affect the efficacy of such practices.

SA controls the production of key antioxidant enzymes in the plant defense system and enhances the activity of enzymes pertaining to ROS detoxification, reflecting the crucial role of this molecule in plant adjustment to abiotic stress (Arif et al., 2020; Mustafa et al., 2018; Yan et al., 2018). Abiotic stresses generate early signal transduction events in plants, which are controlled by ROS, plant hormones, and other molecules (Devireddy et al., 2021). Hormones can trigger ROS production, which influences hormone biosynthesis, transport, and degradation, thus modulating the acclimation of plants to abiotic stress (Devireddy et al., 2021).

SA promotes the activity of antioxidant enzymes to maintain ROS homeostasis under diverse abiotic stresses (Azeem et al., 2023; El-Beltagi et al., 2025; Saleem et al., 2021). This induction helps mitigate oxidative stress by promoting the detoxification of ROS. SA regulates signaling in mitochondria-mediated defense and plant death, but its exact mode of action is unknown (Poór, 2020). SA can also control the transcription of genes encoding antioxidant enzymes. It acts through signaling pathways that involve various transcription factors, leading to the up-regulation of antioxidant defenses in the presence of environmental stressors.

In this process, SA should first bind to some receptors to stimulate a defense response (Spoel & Dong, 2024). SA is perceived by two classes of receptors, NPR1 (non-expresser of

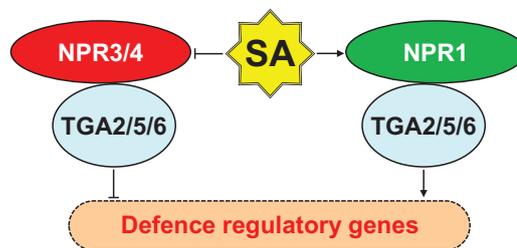


FIGURE 7 Schematic representation of salicylic acid (SA) perception by receptors of the NPR1 family. Both NPR1 and NPR3/NPR4 are SA receptors, but NPR1 functions as a transcriptional co-activator and NPR3/NPR4 serve as transcriptional co-repressors for SA-responsive defense genes. *Source:* Adapted from Zhang and Li (2019).

pathogenesis-related gene 1) and NPR3/NPR4 (Y. Liu et al., 2020). Most research suggests that NPR1 is essential for tying SA and downstream reactions together (Peng et al., 2021). NPR1 controls the SA-responsive genes involved in defense responses by regulating TGA (TGACG-binding) transcription factors (a family of proteins implicated in stress response) (Roychowdhury et al., 2024), as illustrated in Figure 7 according to Zhang and Li (2019). Thus, the SA-mediated signaling engages with the NPR1/3/4 receptors and TGA transcription factors (Rossi et al., 2023). SA causes NPR1 to target precursors and antioxidant proteins for destruction by forming condensates with them (Zavaliev & Dong, 2024). Furthermore, NPR1 has been identified as a crucial factor for cell survival during water deficit stress (X. C. Li et al., 2023). Along with the activation of ROS-generating proteins, NPR1 may be essential to inhibit ROS-degrading proteins, thus maintaining cellular ROS and sustaining stomatal closure (Li et al., 2023). The improved activity of the antioxidant enzymes reflects the defensive role of SA in cellular membranes and its ability to detoxify ROS in stressful conditions (Krantev et al., 2008).

Under conditions of drought, the degree of SA signaling is defined through a complex system, including transcriptional and post-transcriptional regulation of enzymes, as well as modification of key proteins by other molecules. Named for the WRKY domain that identifies a particular motif in target gene promoter regions, the WRKY gene family encodes a broad range of transcription factors that are crucial for many stress responses and developmental processes (Hsin et al., 2022). WRKY transcription factors primarily control tissue structure, root architecture, and stomatal movement to improve plants' resistance to drought (M. Li et al., 2025). In response to drought stress, they take part in the ABA and ROS pathways and affect the expression of genes governing ABA and ROS content (Javed & Gao, 2023). WRKY transcription factors also determine drought stress by modulating the expression of genes related to other phytohormones via various pathways.

Additionally, the NAC (NAM, ATAF1/2, and CUC2) transcription factors family plays a significant role in the drought response mechanism by integrating plant physiological regulation, hormone signal transduction, and gene expression control networks (Han et al., 2025). Some NACs are involved in the regulation of different stress signaling pathways, enabling plants to respond and cope with multiple stresses (Xiong et al., 2025). In the future, a deeper understanding of the roles of NACs in plant immunity might provide support for developing crops with enhanced resistance to abiotic stress.

4.3.3 | SA protects chlorophyll and maintains the photosynthetic capacity

SA was found to protect the chlorophyll content of plants, thus contributing to assimilate production in water-deficient environments. Abiotic stresses can affect different processes in plants, but photosynthesis is a crucial process regulating physiological responses underlying growth and yield (A. Sharma et al., 2020). Chlorophyll is the main component of photosynthesis, which can be affected even by a short-term deficiency of water (Daoqian et al., 2016). As water deficit stress conditions accelerate chlorophyll degradation, chlorophyll content is often used for evaluating the severity of water deficit stress (Ying et al., 2015). Complex metabolic pathways involving a series of interconnected reactions mediated by different enzymes govern chlorophyll biosynthesis and catabolism (X. Li, Zhang, et al., 2024). Low chlorophyll levels have been noted in water-stressed plant species (Khanna et al., 2014; Manivannan et al., 2007; Mafakheri et al., 2010). Lower chlorophyll levels reduce photo-oxidative damage in water-stressed plants, which occurs with obstruction of photosynthesis in excess of light excitation energy (Aranjuelo et al., 2011). Abiotic stress factors can alter gene expression in chlorophyll biosynthesis, leading to lower enzymatic activity, blocking chlorophyll biosynthesis, and lowering chlorophyll content (Abid et al., 2017; Sezgin et al., 2019).

Foliar SA application increases photosynthesis in water-deficient environments, probably by promoting enzyme activity associated with CO₂ uptake at the level of the chloroplast (W. Khan et al., 2003). In this sense, increased photosynthesis after foliar SA application could be associated with increased levels of photosynthetic pigments and high enzymatic activity (Çag et al., 2009). Therefore, SA supply increases the photosynthesis rate and CO₂ assimilation under low moisture (W. Khan et al., 2003). Furthermore, increased photosynthesis after foliar SA application could be attributed to elevated cell sap, which maintains water content in the plants. Foliar SA application can also increase tryptophan concentration, which facilitates conservation of water content in the cells (Hayat et al., 2010). SA can control photosynthesis because

this molecule is involved in stomata functioning (Arfan et al., 2007; W. Khan et al., 2003). Apart from the above-mentioned roles, SA acts as an antioxidant compound in the chloroplasts and safeguards photosynthetic efficiency by scavenging ROS under conditions of abiotic stress. Finally, foliar-applied SA can enhance the de novo synthesis of SA in plants (Szalai et al., 2011).

Overall, quantitative synthesis of the reviewed findings in this section highlights that exogenous SA application confers measurable positive effects on cereal growth under water deficit conditions. The estimated effect ranges showed improvements of 7%–65% in biomass production, 9%–28% in relative water content, and 18%–62% in antioxidant capacity, compared to untreated water-stressed plants. However, the positive effects of SA vary depending on cereal species, genotype, SA rates, and growth conditions (e.g., stress timing and intensity) reported in the reviewed studies. Given this variability, direct numerical comparisons across studies may be misleading.

4.4 | Potential applications of the findings

According to the findings of this review, exogenous SA application promoted growth of cereals in water-stressed environments in terms of biomass production, with only two exceptions (wheat and maize), as explained in a previous section. In the literature, SA was mainly applied as a foliar spray in various water-stressed cereal species, with concentrations mostly ranging between 0.50 and 2.0 mM. This suggests that foliar SA treatments may have the potential for inducing water deficit resistance in cereals.

Research has tested several methods of SA application to improve plant resilience to abiotic stress, such as seed priming, hydroponic delivery, irrigation, or foliar spraying. However, not all these methods are practically suitable for use under field conditions, particularly for large-scale cereal cultivation. A consistent trend across the reviewed cereal studies is that foliar SA was most frequently applied during critical growth windows, most commonly at the vegetative stage (e.g., pre-flowering) or during reproductive development (e.g., at anthesis or grain filling). Beyond cereals, foliar application of SA has been the most widely used method for improving water-stressed sunflower (*Helianthus annuus* L.) growth (Damalas & Koutroubas, 2022). In particular, SA was typically applied once during the vegetative stage or, less frequently, twice during the vegetative and the flowering stages of sunflower. In muskmelon, research has reported seed soaking in SA before sowing as the preferred method for water deficit protection due to its ease of use and simplicity, despite showing similar effectiveness to foliar spraying (Korkmaz et al., 2007). In our view, foliar feeding represents a rapid and targeted strategy that offers flexibility in the administra-

tion of biostimulants, allowing farmers to address problems as needed. Compared with conventional soil applications, foliar spraying is an important development in agricultural techniques, which allows more effective absorption through the leaves and faster plant responses. In certain situations, canopy spraying could be advantageous even if it can be costly. In addition, the flexibility of this method allows farmers to adjust management practices in response to crop requirements and environmental conditions.

SA application rates in cereals appeared more often in the literature in the range of 0.50–2.0 mM across all studies. While low SA concentrations were found to improve physiological and biochemical responses of plants, higher doses can inhibit plant growth. Perhaps improved delivery systems for the controlled release of SA may be effective in maintaining optimal SA concentrations in the long term while minimizing potential toxicity (Kumaraswamy et al., 2019; Polyakov et al., 2023). The targeted delivery of biostimulants to plants can be enhanced by novel formulations using nanotechnology (Khoulati et al., 2025). For example, encapsulation has emerged as an attractive technology for SA delivery in crops facing fungal pressure (Sampedro-Guerrero et al., 2022). Specifically, chitosan-based SA nanoparticles had beneficial effects on maize plants compared to the application of SA alone, as they prevented the burst release of SA to plant cells and averted potential phytotoxicity (Kumaraswamy et al., 2019). Likewise, chitosan-melatonin nanoparticles were found to be a highly promising priming agent for mitigating salinity stress on corn salad (*Valerianella locusta* L.) (Gohari et al., 2024).

Given the differential response of some cultivars to exogenous SA application noted herein, it is necessary to examine the impact of SA across a variety of genetic materials, including cultivars with diverse genetic backgrounds. Previous studies highlight the need for such research. For example, certain maize genotypes showed some variation in their response to the applied rates of SA in terms of maintaining K^+/Na^+ and Ca^{2+}/Na^+ ratios under salinity conditions (Tufail et al., 2013). Similarly, certain tall fescue genotypes reacted diversely to the application of SA in water-deficient environments, with two genotypes demonstrating superior stability and resilience to water deficit stress (Pirnajmedin et al., 2020). In this sense, in addition to improving stress tolerance, external SA treatment may help find genotypes resistant to abiotic stresses, which could be employed as future parents in crossbreeding. This option may be of particular importance given the limitations associated with conventional screening procedures, including the high cost of artificial stress testing and the field variability under natural conditions.

Lastly, the role of SA in ROS-scavenging systems, reported herein, may help in finding tolerant genotypes to water deficit stress through the use of transgenic approaches, for example, by manipulating the levels of antioxidant enzymes. In this

context, molecular breeding targeting transcription factors to improve plant tolerance to water deficit stress can be highly useful (Manna et al., 2021). In recent years, various omics and transgenic strategies have offered opportunities to uncouple resilience to water deficit stress from growth and yield penalties of crops (P. K. Singh et al., 2022). Genomics or proteomics approaches could lead to the identification of genes that are differentially expressed and promote plant tolerance to water stress upon SA application. Such genes can be used as candidates for overexpression or downregulation using, for example, the microRNA approach (A. Singh et al., 2023). The performance of the transgenic plants may be enhanced by overexpressing a single gene that controls tolerance to water deficit stress, gene stacking, and gene pyramiding, which involves overexpressing several genes from various pathways. Nevertheless, future research programs should focus on tolerance to a combination of different stress conditions to reflect field scenarios.

Apart from the above potential applications of the findings of this review, a number of unanswered questions also need to be addressed before SA can be responsibly suggested for practical usage, particularly in field settings, as highlighted below.

4.5 | Future research needs

In this review article, peer-reviewed studies pertaining to the impact of foliar-applied SA on cereals grown in water-deficient environments were collected and analyzed. The majority of the studies noted that foliar-applied SA enhanced the growth parameters of water-stressed cereals in terms of biomass production. Improvement of diverse physiological responses in plants accompanied improvement of growth parameters with foliar SA administration, as discussed earlier. Following the most relevant literature, it was found that exogenous SA applications as a strategy to improve growth in water-deficient environments were mainly studied in wheat, maize, rice, and barley. However, the literature is dominated by wheat and maize, which together account for 39 studies, compared to only 10 studies focusing on rice and barley. This uneven distribution of studies underscores the need to expand future research efforts on rice and barley. Despite this imbalance in research focus across cereals, the beneficial role of SA in enhancing plant growth under water deficit has been recognized across numerous studies, particularly through its involvement in photosynthesis, redox homeostasis, and gene regulation (G. Kaur et al., 2022). Therefore, the use of SA for improving tolerance of cereals to water deficit stress can be a challenge, presenting favorable prospects for future use. Nevertheless, a number of knowledge gaps are revealed based on the above analysis and need to be confronted to advance the efficiency of foliar-applied SA in water-stressed cereals.

First, there is still no established optimal concentration of SA required to induce effective defense responses after foliar application in cereals. The reported application rates vary considerably, and the results are often inconsistent due to differences in plant species, plant developmental stage, mode of application, and environmental conditions at the time of spraying. Regarding environmental conditions at spraying, these can be crucial, as they affect cuticle permeability and droplet efficiency of the spray solution (Puppe & Sommer, 2018). For example, high temperatures can cause rapid water evaporation that leads to shrinkage of the spray droplets, while low temperatures can slow absorption of the spray droplets by the cuticle. Furthermore, low humidity environments also accelerate evaporation of the spray droplets, similar to high temperature effects. Therefore, the optimal concentration of SA for triggering effective defense responses after foliar application, along with the frequency and timing of SA applications, should be better defined under field conditions. Low concentrations of SA advance plant growth in stressful environments, whereas high concentrations of SA can be either detrimental or of no benefit (Damalas & Koutroubas, 2021; Kaya et al., 2023; Rivas-San Vicente & Plasencia, 2011). These contrasting effects of diverse SA concentrations indicate the complex role of this compound in plant growth. Moreover, the difference between low and high concentrations of SA varies with the method of administration and the plant species tested (Pasternak et al., 2019). Such variability can be related to the ontogenic cycle of cereal plants, because each development stage is specifically sensitive to dehydration (Dietz et al., 2021). In this sense, the reported concentrations of SA under field conditions may be contradictory. To address these uncertainties, future studies should systematically evaluate dose–response relationships in cereals under both controlled and field conditions. With reference to the frequency and timing of SA applications, a consistent trend across the reviewed cereal studies is that foliar SA was most frequently applied during critical growth windows, most commonly at the vegetative stage (e.g., pre-flowering) or during reproductive development (e.g., at anthesis or grain filling). However, considering the variability related to the ontogenic cycle of cereal plants, as noted above, future research should target the identification of the optimal timing and frequency of foliar SA applications with regard to specific growth stages. For example, recent research in barley under salinity found that the SA impact depended on the treatment timing, that is, pre-treatment with SA for 24 h versus continuous treatment with SA for 4 days (Torun et al., 2020). Thus, future experiments should also account for species-specific and developmental stage-dependent sensitivity to SA.

Moreover, given that SA was typically administered via foliar sprays in water solution, the optimal conditions for SA to reach its biochemical target have to be studied. For example, variable weather parameters before, during, and

after foliar SA application can weaken the efficiency of the treatment and have a pronounced influence on its efficacy. The inherent limitation of controlled greenhouse conditions to accurately simulate those in the field calls for further research under field conditions. For example, leaf surfaces can be chemically heterogeneous, and this heterogeneity can influence wetting and foliar absorption of solutes (Fernández et al., 2021). In addition, leaf surface roughness and the distribution of chemical compounds are variable, and both factors can affect water deposition on the leaf surface. In addition, crop leaves are covered with different microstructures, leading to difficulties in the deposition of the sprayed droplets (B. Wang et al., 2023). Considering the above, reducing the droplet size can improve foliar deposition, especially for hydrophobic and hyper-hydrophobic crops, such as rice, wheat, and sorghum (*Sorghum bicolor* L.) (Wang et al., 2023). Furthermore, it should be kept in mind that SA has limited solubility in water as compared with organic solvents (Nordstrom & Rasmuson, 2006), which can pose challenges in formulations where water is the primary solvent. Therefore, research on appropriate formulation additives (e.g., solvents and surfactants) for commercial foliar spray products is necessary to improve the SA efficacy by facilitating the penetration of leaf epidermis and translocation through plant membranes.

Second, given the differential response of some cultivars to exogenous SA application noted herein, it is necessary to assess its impact across a wider range of genetic materials, including cultivars with diverse genetic backgrounds and varying levels of tolerance to water deficit stress. Previous research has indicated variation among fennel (*Foeniculum vulgare* Mill.) genotypes in response to drought and foliar application of SA, attributed to genotypic differences in osmolyte accumulation, such as proline and soluble carbohydrates (Askari & Ehsanzadeh, 2015). Similarly, recent research in barley under salinity revealed varying effects of the SA treatment among barley genotypes (Torun et al., 2020), confirming the need of assessing different genetic materials. Indeed, understanding genotypic differences in tolerance to water deficit stress is essential for developing water deficit-resistant cultivars (Vassileva et al., 2023). Therefore, genetic diversity can help sustain desirable traits, such as quality characteristics and tolerance to water deficit stress. For instance, incorporating natural genetic variations that confer differential responses to both water deficit and SA into breeding programs can enrich the genetic base for stress tolerance and improve the capacity to select for high yield under stress. This approach may be of particular importance given the limitations associated with conventional screening procedures, including the high cost of artificial stress testing and the field variability under natural conditions. However, current knowledge in this field remains limited and must be expanded through future research.

Third, the synergistic effects of foliar SA supply with plant nutritional status on crop performance should be defined. Mineral nutritional status affects plant adaptation to adverse environments and mitigates the impact of water deficit stress (Asgher et al., 2014; N. A. Khan et al., 2016; Nazar et al., 2012; Masood et al., 2012). For example, water and nitrogen jointly limit primary productivity in arid and semi-arid regions (Sadras & Richards, 2014) because soil water often regulates nitrogen availability (N. Ali & Akmal, 2022). There is proof that the adverse impacts of water limitation can be lessened by greater nitrogen availability, even though it is unclear what processes are responsible for this effect (Drobnič et al., 2024). SA can shape the nutritional status of plants by influencing plant adaptation to adverse environments. For instance, SA supply can confront shortages of nutrients, which can improve nutrient use efficiency under environmental stress (M. I. R. Khan et al., 2015). Furthermore, SA can promote the absorption of beneficial mineral nutrients and hinder the absorption of toxic nutrients or metals (Kaya et al., 2023). Nevertheless, the communication of different plant parts under unfavorable growth conditions is a complex mechanism involving different signaling molecules. For example, the selectivity mechanism of SA in favoring the absorption of beneficial mineral nutrients and hindering that of the toxic ones remains unclear (Kaya et al., 2023). Unveiling SA signaling and interaction with mineral nutrients in abiotic stress responses remains a difficult problem.

Fourth, the synergistic effects of combining SA with other plant growth regulators or biostimulants on cereals' performance should be examined. SA can significantly reduce or mitigate the negative effects of abiotic stress on horticultural plants (Altaf et al., 2023; Yang et al., 2023) as well as on cereals, as reviewed herein. It engages in intricate crosstalk with other phytohormones under abiotic stresses and the nuances of this interaction vary depending on the circumstance and have multiple dimensions (A. Ali et al., 2024; Elsisy et al., 2024). Although much work has been done on the function of phytohormones in plant reaction to environmental stress, further work is still required to improve comprehension of the action mechanism of these molecules in crop tolerance under stressful growth conditions. There are more facets of SA-mediated defensive signaling than previously believed, ranging from SA production and homeostasis to redox regulation and hormonal crosstalk (Ullah et al., 2023). New discoveries of phytohormones make this understanding more complex. Moreover, the function of phytohormones is linked to multiple interactions with each other in stressful conditions. When some phytohormones are applied to plants, the host metabolism, defense mechanisms, and gene expression are reprogrammed (P. Ghosh & Roychoudhury, 2024). Given the great complexity of phytohormone crosstalk (Tian et al., 2024), this topic is not discussed in the present review article, as the aim was to facilitate comprehension of the main

physiological effects of SA application on cereal growth. Nevertheless, further research on phytohormones crosstalk in cereals is needed to better understand the mechanisms of growth regulation.

Fifth, even when the above gaps are filled, the economic feasibility of using SA as a foliar treatment in large-scale agricultural production systems should be defined. The economic feasibility of treatments is the most important factor when making suggestions to farmers. Indeed, this parameter is often the decisive factor for the adoption of any innovation or technique on a large scale in the farming community. However, the economic feasibility of SA-based foliar applications is not yet well established. In fact, cost-effectiveness under field conditions remains uncertain, as it depends on multiple factors, such as number of applications, yield responses, and product formulation costs, as well as labor. Nevertheless, a detailed economic analysis of SA foliar application costs per hectare is beyond the scope of this review article, where the focus is on the physiological effects of exogenous SA application on the growth of water-stressed cereals rather than economic considerations.

In addition to the abovementioned gaps, significant advances have been made in the field of omics technologies, which have emerged as powerful tools for building a resilient agricultural future and elucidating intracellular processes within plant cells (Joshi et al., 2024; M. H. Saleem et al., 2025). Although omics research holds promise for unraveling complex biological systems, it also faces serious technological and methodological hurdles that fall beyond the scope of this review.

4.6 | Strengths and limitations

This review article relies on the most relevant peer-reviewed evidence in the literature regarding foliar SA applications in cereals grown in water-deficient environments, achieving full coverage of the latest developments in the field. The main strength of this work is the critical look at the most relevant experimental evidence of foliar SA application on cereals, summarizing key findings relevant to the topic from each of the major studies. By integrating findings from all relevant studies on cereals, the present review article reveals interesting research questions with a power that no single study has. Another strength of this review article is that, apart from summarizing the relevant literature on the topic, it also considers the overall picture that emerges, and thus it uncovers areas in which more research is needed, as commented on in the previous sections. Another strength of this review article is that it focuses on foliar-applied SA on cereals from an agronomic point of view, which can help in determining whether the SA impact is consistent across research and identifying the future studies to prove the effect. Most studies deal with the molec-

ular mechanisms of SA impact under abiotic stress, but a few studies are related to practical applications. The above information can be useful in terms of optimizing the use of foliar SA applications in cereals.

Concurrently, there are some weaknesses in this review article that must be noted to better assess the major findings and their usefulness. First, the article set some prerequisites for the selection of the peer-reviewed literature evaluated (as noted in previous sections), which might have caused some bias. For example, to facilitate comprehension, this review article considered water deficit events of different intensity and duration occurring at any point of the plant ontogenetic cycle. This was because different water deficit types have different characteristics, and episodes of water deficit might range in duration, timing, and intensity (Passioura, 2012). Furthermore, the assessment of water deficit impact on crops can be fairly subjective, especially because water deficit is driven by precipitation, temperature, vapor pressure, solar radiation, and their complex interactions (Leng & Hall, 2019). However, the selection of the literature in this article facilitates clarity and comprehension of the SA role as a stress alleviator in cereals, and any potential bias of this kind does not distort the general trends of the literature concerning the effects of foliar SA application on cereals in water-stressed environments. Second, we considered all studies discussed in this article of equal importance, although some studies might be less reliable than others, potentially due to methodological or evaluative shortcomings, which might result in biased findings. However, the selection of the literature captures the real status of SA use in cereals, and any potential bias of this kind does not distort the general trends observed in the literature. Third, some studies can vary in their relevance to the review question (e.g., by being conducted at different spatial scales), which was accounted for in the current synthesis by focusing on foliar SA application in cereals. Moreover, given that the majority of studies were carried out under controlled conditions, this may limit the relevance of findings in real-world settings. In this regard, research under field conditions should be conducted to document and validate best practice recommendations in the field. Finally, it should be kept in mind that the complexity of cereal reproduction and the variable responses to environmental stress hinder the establishment of a relationship between successful plant reproduction and high yield levels in stressful conditions (Barnabas et al., 2008).

5 | CONCLUSIONS

In this review article, the state-of-the-art in peer-reviewed literature on the biological functioning of exogenous SA application in water-stressed cereals is presented. To this

end, both quantitative and qualitative analyses of this field of research have been provided. Exogenous SA was primarily applied as a foliar spray in water-stressed cereals, at a variety of rates, with 0.50–2.0 mM being the most frequently reported across all cereals. Except for one study on wheat and one on maize, the remaining studies reported that exogenous SA application promoted growth, mainly by enhancing biomass production under water deficiency. The beneficial effect of exogenous SA application was primarily associated with (i) enhanced osmolyte accumulation, promoting water retention, (ii) improved activity of antioxidant enzymes, maintaining intracellular redox homeostasis, and (iii) chlorophyll protection, preserving photosynthetic efficiency in water-deficient environments.

Foliar applications of SA hold promise as a practice for improving tolerance of cereals to water deficit stress, based on experimental evidence from different cereals. A future research roadmap should involve studies aiming at determining the optimal concentration, frequency, and timing of exogenous SA applications for enhancing the defense of water-stressed cereals. Considering the variability present in the available genetic material, genotype-specific dose optimization is necessary. Furthermore, research and development of SA delivery systems based on nanocarriers are still needed. Given the complex role and behavior of SA, further work is required on SA interaction with other plant hormones (e.g., melatonin and JA) and plant growth regulators, taking into consideration the overall physiological status of the plants (e.g., growth stage and nutritional status) during application. In any case, foliar applications of SA aimed at increasing resistance to water deficit and reducing yield loss in cereals need to be assessed for efficacy and economic viability in the field. The synthesis provided in this review may serve as a valuable reference for both researchers and practitioners in the field of crop stress physiology and water deficit management.

AUTHOR CONTRIBUTIONS

Christos A. Damalas: Conceptualization; data curation; methodology; writing—original draft; writing—review and editing. **Spyridon D. Koutroubas:** Conceptualization; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The raw data presented in this study are available on request from the corresponding author.

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