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## Review

# Role of Salicylic Acid in Combating Heat Stress in Plants: Insights into Modulation of Vital Processes

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## Abstract

In the present era of climate change and global warming, high temperatures have increased considerably, posing a threat to plant life. Heat stress affects the biochemistry, physiology and molecular makeup of the plant by altering the key processes, i.e., photosynthesis, respiration and reproduction which reduces its growth and development. There is a dire need to manage this problem sustainably for plant conservation as well as the food security of the human population. Use of phytohormones to induce thermotolerance in plants can be a sustainable way to fight the adversities of heat stress. Phytohormone-induced thermotolerance proves to be a compelling approach to sustainably relieve the damaging effects of heat stress on plants. Salicylic acid (SA) is an essential molecule in biotic and abiotic defense response signal transduction pathways. When supplied externally, it imparts heat stress tolerance to the plants by different means, viz., increased Heat Shock Proteins (HSP) production, Reactive oxygen species (ROS) scavenging, protection of the reproductive system and enhancing photosynthetic efficiency. The effect of SA on plants is highly dependent on the concentration applied, plant species, plant age, type of tissues treated, and duration of the treatment. The present review paper summarizes the mechanism of thermotolerance induced by salicylic acid in plants under heat stress conditions. It includes the regulatory effects of SA on heat shock proteins, antioxidant metabolism, and maintenance of  $\text{Ca}^{2+}$  homeostasis under heat stress. This review combines the studies conducted to elucidate the role of SA in the modulation of different mechanisms which lead to heat stress tolerance in plants. It discusses the mechanism of SA in protecting the photosynthetic machinery and reproductive system during high-temperature stress.

**Keywords:** antioxidant system; heat shock proteins; heat stress tolerance; photosynthesis; salicylic acid

## 1. Introduction

Salicylic acid (SA) is a hepta-carbon phenolic compound used effectively as an analgesic for more than 2000 years. It occurs in nature as an endogenously synthesized ubiquitous plant growth regulator. Plants synthesize SA through two main pathways: phenylalanine and isochlorogenic acid, which are part of the shikimic acid pathway [1,2]. SA balances plant growth and development along with critical physiological processes [3]. It was not before 1987 when SA (earlier known as calorigen) caused thermogenesis in treated flowers of voodoo lily (*Sauromatum guttatum*) [4]. Being a plant signaling molecule, it has a role in local and systemic plant defense responses against pathogens through its direct or indirect involvement in sig-

naling networks [5]. It helps in providing resistance to biotic and tolerance toward abiotic stress in plants [6,7], such as temperature extremes [8], heavy metals [9], drought [10–12], osmotic [13] and salinity [14]. The stress caused by heat is a potential global risk to food security caused due to accelerated temperature and anthropogenic activities, which have aggravated the problem by degrading the agricultural system. Heat stress influences the plant from seed germination to maturity and causes drastic economic yield losses. In plants, many interconnected changes like morpho-anatomical, physiological and biochemical modifications occur due to the adverse effects of transient or constant high temperature. In a broad sense, these changes could be categorized as direct and indirect injuries. The continuous high temperature may cause immediate injuries,



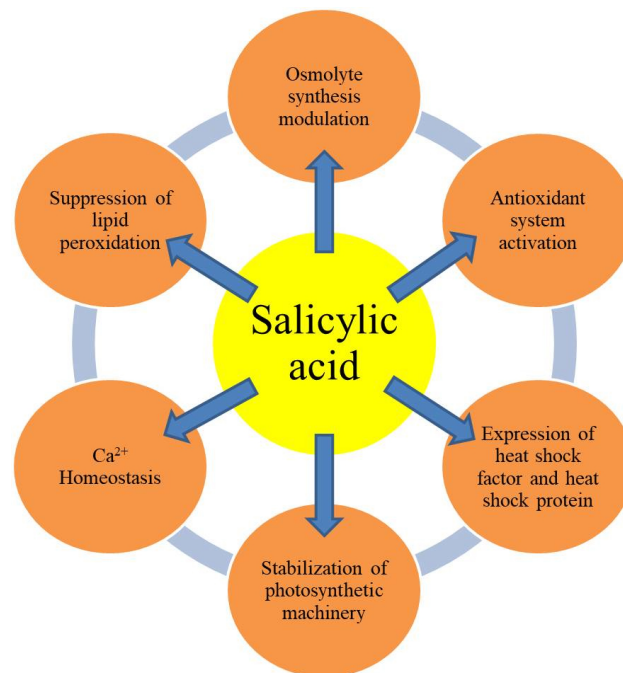
including protein denaturation, aggregation, and increased fluidity of membrane lipids. On the other hand, slow or transient heat produces indirect damage such as inactivation of chloroplastic and mitochondrial enzymes, suppression of protein synthesis, protein degradation, loss of membrane integrity, and photosynthetic machinery arrest [15].

Numerous approaches are being used to enhance crop tolerance and reduce the negative impacts of heat stress on plants [16–18]. Exogenous application of plant growth regulators such as Absciscic acid (ABA), Jasmonic acid (JA), SA, and others can induce thermotolerance [19,20]. The SA can be applied through different means, including seed priming, irrigation or foliar spray [21,22]. SA initiates the abiotic stress tolerance mechanisms when provided exogenously to stressed plants. The influence of SA on the plant is dose-dependent, where low and high SA concentrations can result in different outcomes for the same plant species. The specific high or low concentration of SA treatment depends on many factors i.e., the duration of the treatment, plant species, plant age, and treated plant part [23].

Thermo protection using SA was first induced in mustard with low concentration (0.01–0.1 mM) [24]. SA can have different effects based on concentration given and may even vary on the basis of plant species studied [25,26]. The exogenous SA application can increase the levels of endogenous SA (in free or glycosylated forms) and mimic heat acclimation. Hence, both the acclimation process and external application of SA can improve the plant survival under stress [27]. Larkindale and Knight [28] concluded that SA is vital in protecting the plant from heat-induced oxidative stress. SA signaling helps in acquiring basal thermotolerance in Arabidopsis and insulates against heat stress and the subsequent recovery [29]. It can also increase levels of Phenylalanine Ammonia Lyase (PAL) mRNA, new PAL protein production, and accumulation of considerable amounts of phenolics, all of which contribute to thermotolerance [30]. In *Triticum aestivum*, heat stress was alleviated using 0.5 mM SA by reducing the activity of 1-amino cyclopropane carboxylic acid synthase (ACS) and restricting ethylene formation under heat stress [31]. Plant physiology and yield attributes were improved under heat stress by seed priming and external SA application [32]. Studies have also attempted to annotate functional components and signaling networks linked with molecular mechanisms involved in SA-mediated heat stress response in plants [33].

This review paper summarizes the studies conducted to better understand the SA-induced plant tolerance to heat stress (Table 1, Ref. [24–26,31,32,34–65]). Therefore, those aspects are emphasized that possibly underpin heat stress tolerance in the presence of SA and its crosstalk with other factors indulged in the signal transduction pathway. The primary focus is to support the important functions of SA (applied externally) in modulating different plant systems to achieve heat stress tolerance (Fig. 1). Various subsections briefly discuss the interconnections of SA with heat

shock proteins, photosynthetic machinery, involvement of SA in the signaling of reactive oxygen species (ROS) along with the alteration of antioxidants, major osmolytes like proline,  $\text{Ca}^{2+}$  homeostasis, and lipid peroxidation.



**Fig. 1. Interaction among SA and various components of the plant system contributes to heat stress tolerance.**

## 2. SA Protects the Plant Reproductive System from Heat Stress

The occurrence of high-temperature stress in the course of the reproductive phase significantly affects the production of pollens and seeds in some botanical species, viz. rice [66], wheat [67], tomato [68], cowpea [69] and Arabidopsis [70]. Heat stress is not suitable for flower development, especially the development of stamens. The extent of vulnerability varies between male and female reproductive systems; female reproductive organs are less susceptible to heat stress than male reproductive organs, as evidenced by the significant susceptibility of tapetal cells present in the anther [71]. The most sensitive events in the reproductive phase of plants are pollen mother cells (PMC) meiosis, microspore development, tapetum development, anther dehiscence/pollen release, and the fertilization process [72,73]. Degeneration of microspores and increased cell size (hypertrophy) of tapetum are the most prevalent effects which result in male sterility [74]. In rice, exposure to heat for 4 days or more during the early stages of anther development caused the tapetum cells to degrade prematurely and to undergo programmed cell death (PCD), which resulted in male infertility [75]. Additionally, downregulation of some crucial genes linked to male sterility, viz.

**Table 1. Summary of representative studies on the salicylic acid (SA)-mediated control of heat stress in plants**

Species	Applied SA concentration	Mode of application	Parameters studied	Reference
<i>Sinapis alba</i>	10–500 $\mu\text{M}$	Foliar spray	$\text{H}_2\text{O}_2$ content, catalase	[24]
<i>Sinapis alba</i>	100 $\mu\text{M}$	Foliar spray	Endogenous SA level, antioxidant metabolites, antioxidant enzymes	[47]
<i>Solanum tuberosum</i>	$10^{-6}$ and $10^{-5}$ M	Culture medium	$\text{H}_2\text{O}_2$ content, catalase	[54]
<i>Nicotiana tabacum</i>	10 and 100 $\mu\text{mol}\cdot\text{L}^{-1}$	Culture medium	$\text{H}_2\text{O}_2$ content, antioxidant system	[25]
<i>Phaseolus vulgaris</i> and <i>Lycopersicon esculentum</i>	0.1–0.5 mM	Seed priming	Survival percentage	[26]
<i>Nicotiana tabacum</i>	70 $\mu\text{M}$	Protoplast incubation	Hsp 70	[55]
<i>Agrostis stolonifera</i>	10 $\mu\text{mol}\cdot\text{L}^{-1}$	Foliar spray	Turf quality, leaf photosynthetic rate, TBARS (Thiobarbituric Acid Reactive Substances), antioxidant enzymes	[43]
<i>Triticum aestivum</i>	1 mM	Seedling treatment	Dry weight of seedlings, $\text{H}_2\text{O}_2$ content, antioxidant enzymes	[49]
<i>Cicer arietinum</i>	100 $\mu\text{M}$	Foliar spray	Relative injury of membranes, protein and proline content, antioxidant enzymes	[50]
<i>Poa pratensis</i>	0, 0.1, 0.25, 0.5, 1 and 1.5 mmol	Foliar spray	Turf quality, leaf water content, AOS (active oxygen species) production, $\text{O}_2^-$ generating rate, $\text{H}_2\text{O}_2$ content, antioxidant enzymes	[48]
<i>Pisum sativum</i>	100 $\mu\text{M}$	Foliar spray	Membrane marker assay, $\text{PIP}_2$ -PLC (PI bisphosphate - Phospholipase C) and PAL (Phenylalanine ammonia lyase) activity, endogenous SA level, MDA (malondialdehyde) content	[56]
<i>Cucumis sativa</i>	1 mM	Foliar spray and nutrient solution	Lipid peroxidation, chlorophyll fluorescence, antioxidant enzyme activity	[40]
<i>Vitis vinifera</i>	100 $\mu\text{mol}\cdot\text{L}^{-1}$	Foliar spray	Relative electrolyte leakage, TBARS, antioxidant metabolites, antioxidant enzymes, $\text{Ca}^{2+}$ homeostasis	[44]
<i>Vigna radiata</i>	0.5 and 1 mM	Foliar spray	$\text{H}_2\text{O}_2$ content, MDA content, membrane leakage, antioxidant enzymes, carotenoid content	[57]
<i>Lycopersicon esculentum</i>	0.1 mM	Foliar spray	Hsp 70, Hsf A1, Hsf A2, Hsf B1, Hsf-DNA binding	[36]
<i>Brassica juncea</i>	$10^{-5}$ M	Foliar spray	Plant growth, chlorophyll and photosynthesis measurements, leaf water potential, proline content, antioxidant enzymes, carbonic anhydrase, nitrate reductase, leaf nutrient status	[58]
<i>Brassica</i> spp.	10 and 20 $\mu\text{M}$	Foliar spray	Electrolyte leakage, total soluble sugar, protein profiling, soluble neutral invertase, antioxidant enzymes	[59]
<i>Arabidopsis thaliana</i>	250 $\mu\text{M}$	Culture medium	Hsp 101 and Hsp 17.6	[37]
<i>Vitis vinifera</i>	100 $\mu\text{M}$	Foliar spray	Net photosynthesis rate, substomatal $\text{CO}_2$ concentration, stomatal conductance, PSII (Photosystem II) electron transport, energy dissipation, Rubisco activation state and Hsp 21	[38]

Table 1. Continued

Species	Applied SA concentration	Mode of application	Parameters studied	Reference
<i>Triticum aestivum</i>	0.5 mM	Foliar spray	Proline metabolism enzyme, TBARS, H <sub>2</sub> O <sub>2</sub> content, quantum yield efficiency of PSII, photosynthetic NUE (nutrient use efficiency), N metabolism, leaf osmotic potential, water potential, water use efficiency, Rubisco activity, ethylene metabolism	[31]
<i>Triticum aestivum</i>	0.1, 0.3 and 0.5 mM	Foliar spray	Chlorophyll content, chlorophyll fluorescence, net photosynthesis rate, <i>psbA</i> transcription, lipid peroxidation, O <sub>2</sub> <sup>-</sup> generating rate, H <sub>2</sub> O <sub>2</sub> content, malondialdehyde content (MDA), antioxidant enzyme activities	[41]
<i>Cicer arietinum</i>	0.2, 0.4, 0.6, 0.8 and 1.0 mM	Foliar spray	Heat tolerance assessment, H <sub>2</sub> O <sub>2</sub> content, CAT (catalase), polyphenol oxidase (PPO), protein profiling	[60]
<i>Triticum aestivum</i>	100 mM	Foliar spray	Differential protein profiling, heat responsive transcription factors, stress associated genes, soluble starch synthase activity, morphology of starch granule and starch content	[35]
<i>Solanum lycopersicum</i>	0.25 and 0.5 mM	Foliar spray	Growth and yield characteristics, chlorophyll content, carotenoid content, total soluble sugar, proline content, MDA content, POX (peroxidase) and PAL activity	[61]
<i>Gossypium hirsutum</i>	0, 0.5, 1.0 and 1.5 mM	Foliar spray	H <sub>2</sub> O <sub>2</sub> content, MDA, proline content, total soluble protein content	[52]
<i>Matricaria chamomilla</i>	0, 1, 10, 26 and 100 mg·L <sup>-1</sup>	Foliar spray	Physiological characters, chlorophyll content, free proline concentration, essential oil	[62]
<i>Brassica juncea</i>	0, 50, 100 and 150 ppm	Foliar spray	Relative water content, photosynthetic parameters, chlorophyll content, heat susceptibility index, membrane stability index	[63]
<i>Zea mays</i>	10–800 µM	Foliar spray	Seedling growth, antioxidant metabolites and antioxidant enzymes	[45]
<i>Oryza sativa</i>	0.01, 0.1, 1, 10 and 50 mM	Foliar spray	Pollen viability, antioxidant enzymes, H <sub>2</sub> O <sub>2</sub> content, ROS (Reactive oxygen species), MDA content, caspase3 activity, q-PCR analysis, seed setting rate	[34]
<i>Triticum aestivum</i>	10 <sup>-4</sup> M	Seed priming and foliar spray	Electrolyte leakage, chlorophyll content, proline content, soluble sugar, soluble protein, yield attributes	[32]
<i>Triticum aestivum</i>	10 %	Foliar spray	Leaf growth, yield attributes, relative water content, chlorophyll content, proline content, total soluble sugar, total phenolics, antioxidant enzymes, grain quality	[53]
<i>Oryza sativa</i>	100 mg·L <sup>-1</sup>	Foliar spray	Seedling parameters, total soluble sugar, total soluble proteins, nitrate reductase, nitrite reductase, uptake of nutrients (N,P,K, Mg)	[64]
<i>Mentha × piperita</i> and <i>Mentha arvensis</i>	2, 3 and 4 mM	Foliar spray	Relative water content, antioxidant enzymes, essential oils	[51]

Table 1. Continued

Species	Applied SA concentration	Mode of application	Parameters studied	Reference
<i>Solanum lycopersicum</i>	1 mM	Foliar spray	Photosynthetic efficiency, water use efficiency, electrolyte leakage, antioxidant enzymes, chlorophyll content, MDA content, H <sub>2</sub> O <sub>2</sub> content, proline content	[42]
<i>Euphorbia pulcherrima</i>	200 and 400 µM	Foliar spray	Electrolyte leakage, MDA content, antioxidant enzymes, plant appearance	[65]
<i>Capsicum annuum</i>	0, 0.002, 0.01, 0.05 and 0.25 mM	Petri plate medium and foliar spray	Antioxidant content and enzymes, seedling parameters, relative electrical conductivity, relative water content, root activity, MDA content, soluble sugar and protein, proline content, chlorophyll content, photosynthesis parameters	[46]
<i>Lablab purpureus</i>	0.5 and 1 mM	Foliar spray	Photosynthetic efficiency, chlorophyll content, leaf water content, electrolyte leakage, yield attributes, carotenoid content, MDA content, proline content, H <sub>2</sub> O <sub>2</sub> content, antioxidants and enzymes, pollen viability, anatomical changes in leaves, expression analysis of stress-responsive genes	[39]



YY1, YY2, TGMS, and tms5 due to heat stress have also been reported in rice [76]. Similarly, the *YUCCA* gene in Arabidopsis exhibited lower expression under heat stress conditions, particularly in tapetum cells and PMC, resulting in male fertility reduction [77].

SA has successfully reduced the harmful impacts of this stress in vegetative stages, but the reproductive stage is far less explored in this respect. Most works on the protective effect of SA during the reproductive stage have been performed predominantly on rice than on any other plant species. Fu *et al.* [78] reported the protective results of SA in alleviating some damages caused in the process of spikelet differentiation by heat stress in rice. SA increased the actual light quantum efficiency and  $P_n$  of leaves under heat stress. In this regard, Zhang *et al.* [79] concluded that in rice under heat stress, the soluble sugars, antioxidant enzymes, and IAA (Indole acetic acid) were higher in SA treated plants and prevented spikelet degeneration due to heat. In Arabidopsis, SA alters the activities of apical cells. Hence, it has a role in plant flowering and the growth of pollen tips [80]. Feng *et al.* [34] observed that the application of SA provides heat resistance to rice at the PMC meiosis stage. It also prolonged the viability of pollen grains besides improving seed-setting. The possible heat tolerance mechanism involves SA-mediated scavenging of excess ROS present in anthers; here, SA helped prevent tapetum degeneration caused by heat stress by inhibiting the caspase-3 activity and PCD in anthers.

Furthermore, genes involved in tapetum development, viz. *EAT1*, *MIL2*, and *DTM1* were also engaged in heat tolerance mechanisms mediated by SA. The pathway might have also been dependent on hydrogen peroxide ( $H_2O_2$ ) because higher levels of  $H_2O_2$  were correlated with the pollen viability and lower levels of MDA in response to SA treatment at the PMC meiosis stage of rice under heat stress.

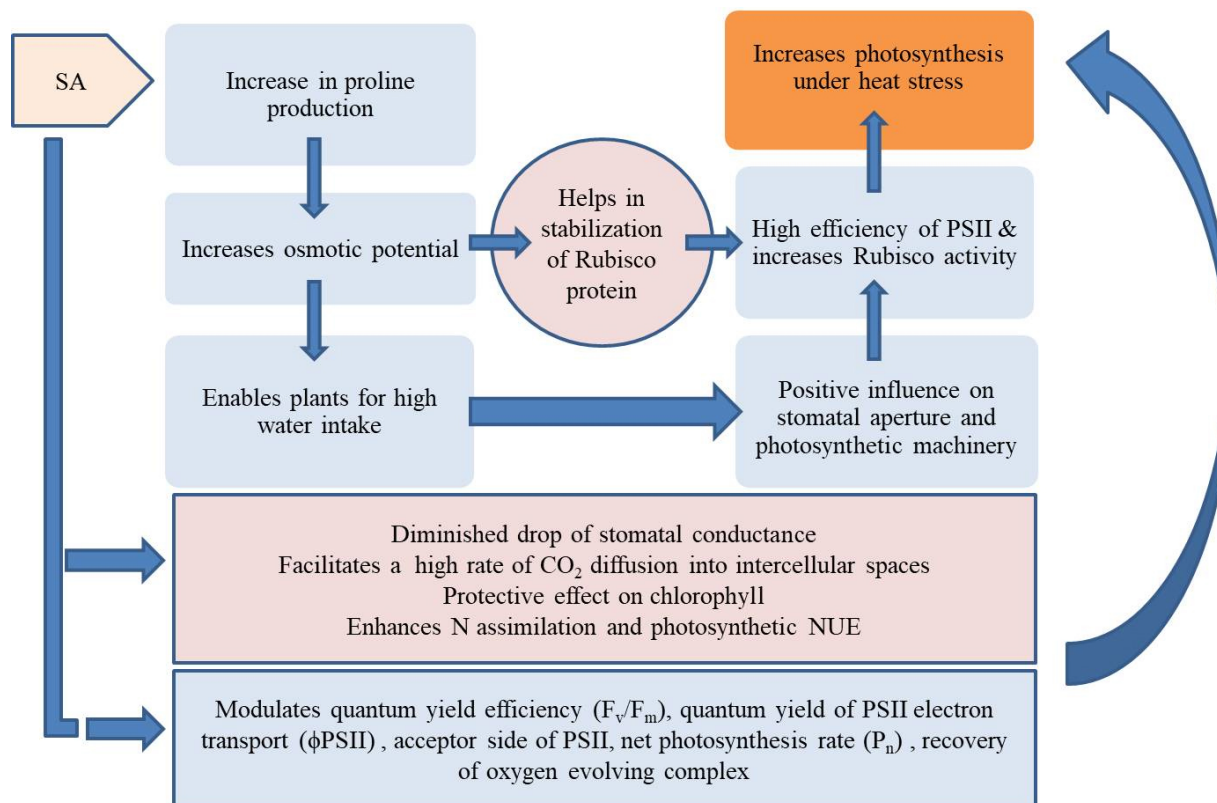
### 3. Effects of SA on Heat Shock Protein Synthesis

Heat shock proteins (HSPs) are multi-family proteins that act as chaperones in nature and play a key role in the survival mechanism of organisms under various stresses [81]. They exist in five families based on their molecular weight, namely HSP100, HSP90, HSP70, HSP60/40, and HSP20 [82]. Heat shock proteins from all of these families have distinct and essential roles in different developmental processes in plants, especially under abiotic stress conditions [83]. Depending on their location, substrate selectivity, and transcript level pattern, HSPs can perform additional tasks. Small heat shock proteins (sHSPs) express when plants are subjected to heat stress. The sHSPs protect photosystem II (PS II) and the whole electron transport chain by binding to thylakoid membranes [84]. Many processes involving HSP101 and class I & II sHSPs help acquire thermotolerance [85]. Kumar *et al.* [35] discovered that when SA was applied to wheat plants under

stress, it increased the expression of transcription factors [Heat stress transcription factors (HSF4 and HSF7) and Drought responsive element binding protein (DREB)] as well as heat-responsive proteins [HSP17, oxygen-evolving enhancer protein, ATP synthase small subunit, rubisco activase, cyclin-dependent protein kinase (CDPK), and superoxide dismutase (SOD)]. Also, the SA-treated plants exhibited a lesser reduction in starch content and soluble starch synthase (SSS) alongside protection to the starch granule morphology of thermotolerant wheat cultivar (C 306) compared to susceptible (PBW 343). SA increased the accumulation of HSP/HSC70 in tomato seedlings [36]. However, the presence only of SA did not affect the HSP70 level, and heat shock was also required. In both SA and heat shock, the seedlings showed a high Hsf-DNA binding, suggesting that the SA modulates Hsf, leading to the HSP70 accumulation. It also enhances the expression of hsp70, hsfA1, hsfA2, and hsfB1. Earlier, Cronjé *et al.* [86] also observed while working with tobacco protoplasts that SA alone did not influence HSP70 proliferation. SA could either induce or inhibit HSP expression depending on ambient conditions. It was observed that at room temperature, i.e., 26 °C, it did not influence the expression of hsp101 and hsp17.6. However, at mild heat shock temperature (37 °C), it remarkably reduced the induced expression of hsp101 and hsp17.6 [37]. A clone designated Oshsp18.0 CII is rare in class II sHSPs and gets induced by SA [87]. However, SA did not cause Oshsp18.0 CII protein accumulation, or the level was too low to be detected through western blot analysis. Wang *et al.* [38] observed the accelerated recovery of plants when treated with SA and noticed high levels of HSP21 during the recovery period. SA also enhanced the expression of hsp17, and this expression was higher in thermotolerant (C 306) in comparison to thermosensitive (PBW 343) wheat [35]. Similarly, Rai *et al.* [39] also observed up-regulated expression of hsf in *Lablab purpureus* under heat stress.

### 4. Relation between SA and Photosynthetic Machinery

Photosynthesis is a delicate process in green plants [88]. When stress hits a plant, photochemical reactions are the primary site of injuries in the thylakoid lamellae in chloroplast stroma [89]. As an impact of heat stress, the dissociation of the oxygen-evolving complex (OEC) imbalances the flow of electrons from OEC to the acceptor of PS II [90]. Other susceptible reaction center parts, such as D1 and D2 proteins, are also impaired by heat stress [91]. Higher quantum yield efficiency ( $F_v/F_m$ ) and quantum yield of PS II electron transport ( $\phi PS II$ ) were observed for foliar spray treatment of 1 mM SA than through nutrient solution and combined (nutrient + foliar) treatment in *Cucumis sativa* [40]. The net photosynthetic rate ( $P_n$ ) responds differently to the application of SA under normal and stressed conditions. For example, in grape plants under average



**Fig. 2. SA mediated protection of Photosystem II and enhanced photosynthesis under heat stress.**

temperature, the dose of 100  $\mu\text{M}$  SA did not change the  $P_n$  significantly. At the same time, it significantly reduced the  $P_n$  under heat stress and promoted the  $P_n$  in the recovery period [38]. Also, the SA application significantly improved the  $W_k$  ( $F_{300\mu s} - F_o$ )/( $F_j - F_o$ ); which represent the damage to OEC and the Rubisco activation state.

Additionally, the PS I was more protected during the recovery phase than the control. When SA is applied, photosynthesis is protected against heat stress by a combination of physiological and biochemical mechanisms, including increased water potential (due to Rubisco protein stabilization), higher nitrogen uptake, and higher N allocation to Rubisco protein, i.e., higher photosynthetic nitrogen use efficiency and reduced stress ethylene production with elevated  $F_v/F_m$  of PS II [31,92]. SA also limits the decrease in net photosynthesis, stomatal conductance, and carbon dioxide ( $\text{CO}_2$ ) concentration between cells in heat-stressed plants, which ultimately preserves (at least partially) photosynthesis. Wang *et al.* [41] reported that a foliar spray of 0.3 mM SA reduced chlorophyll's degradation, which might be the protective effect of SA to limit the damage caused by high heat and light. It also inhibited decline in  $F_v/F_m$ ,  $F_v/F_o$ , electron transfer rate to PS II (ETR), and  $P_n$ , indicating that exogenous SA can alleviate photoinhibition caused by heat and high light stress in wheat leaves at the time of grain filling. SA alleviated the suppression in psbA (encoding D1 protein) transcription caused by heat and high light stress.

According to Jahan *et al.* [42],  $F_o$ ,  $F_v/F_m$ ,  $Y(\text{II})$  (effective photochemical quantum yield of PS II),  $Y(\text{NPQ})$  (regulatory energy dissipation quantum yield of PS II), and  $Y(\text{NO})$  (non-regulatory energy dissipation quantum yield of PS II) all significantly decreased when tomato seedlings were exposed to high temperatures. When SA was applied, these parameters increased. Thus, SA releases the energy from the photosynthetic components as heat and photoinhibition while also rebuilding the photosynthetic machinery to function properly. The exogenous application of SA increased the photosynthetic efficiency of alfalfa [93]. All findings discussed above support the hypothesis that the protection induced by SA in PS II during heat stress and recovery involves several features of PS II function, influencing OEC and PS II reaction center. SA repairs the damaged photosynthetic machinery. Fig. 2 represents a schematic diagram illustrating SA-mediated protection of Photosystem II and enhanced photosynthesis during heat stress.

## 5. Effect of SA on Lipid Peroxidation

Stress causes injuries to membranes, which leads to oxidative damage. Lipid peroxidation is indicated by measuring thiobarbituric acid reactive substances (TBARS) concentration, a standard assay for oxidative membrane damage [94]. A large proportion of linolenic acid (polyunsaturated fatty acids) in the leaves is confined to the thylakoid glycolipids. The oxidative degradation of linolenic



acid specifically leads to TBARS formation. Therefore, its development in the leaves is a possible measure of peroxidative harm to the chloroplast membrane [95]. Elevated amounts of TBARS were present in plants exposed to high oxidative stress levels. SA pre-treated plants had lower TBARS than untreated plants in *Agrostis stolonifera* [43]. This ultimately led to 3-fold lower oxidative damage than controls by the end of treatment. Specific proteins are protected by the foliar spray of SA, characterized by reduced TBARS which results in reduced peroxidation [40]. In a study on grape plants under heat stress, SA pre treatment resulted in reduced TBARS content and protected the plants [44]. Similarly, Khan *et al.* [31] also observed that SA treatment reduced TBARS content in heat-stressed wheat plants.

Malondialdehyde (MDA) is a marker of oxidative stress resulting from ROS degeneration of polyunsaturated lipids under stress conditions. When SA was applied to stressed wheat plants, the MDA levels were considerably reduced compared to plants only subjected to stress [41]. It also enhanced the decline of MDA content in the recovery period. The MDA content declined with 1.5 mM SA, which helped develop thermotolerance in cotton seedlings. The MDA content of maize seedlings was reduced under heat stress due to the foliar spray of SA [45]. Declined MDA content was also reported by Zhang *et al.* [46] in ornamental pepper by SA foliar spray under heat stress. This could be credited to an enhanced antioxidant defense system and alleviated heat stress-induced membrane damage.

## 6. Modulation of Antioxidant Metabolism by SA

In the typical aerobic metabolism of plants, ROS like superoxide ( $O_2^-$ ) and  $H_2O_2$  are frequently produced and scavenged. Minimum levels of ROS have important signal transducing roles and can help arrange the plant responses to various stresses. For example, heat stress can accelerate the respiratory and photosynthetic electron transport systems. This causes an imbalance between the generation and scavenging of ROS [96], eventually leading to oxidative stress. Cheng *et al.* [97] suggested that SA acts as an antioxidant. SA (endogenous and exogenous) regulates the antioxidant metabolism and has tight control over cellular ROS because of its various actions [98]. In higher quantities, ROS are harmful to plants [99] and are controlled by antioxidant systems. The antioxidant system consists of enzymatic and non-enzymatic components. Higher efficiency of antioxidative systems causes higher resistance to environmental stress.

Externally applied SA controls antioxidant enzymes activities and increases plant tolerance to abiotic stress. For example, an increase in the concentration of  $H_2O_2$  and a decrease in catalase activity (CAT) were observed in mustard seedlings when treated with 0.01 mM SA and acclimated at 45 °C for 1 h [24]. Similarly, Dat *et al.* [47] found that 100

$\mu$ M SA lowered the ascorbate ratio (reduced to oxidized) in mustard seedlings. Initially, the reduced glutathione (GSH) and oxidized glutathione (GSSG) levels decreased, then they increased, accompanied by higher glutathione reductase (GR) activity, which maintains the glutathione pool in a reduced state. This adjustment in the redox state of the pool indicates its involvement in acclamatory stress signaling. In this regard, dehydroascorbate reductase (DHAR) and monodehydroascorbate reductase (MDHAR) dropped. In contrast, ascorbate peroxidase (APX) activity increased, which resulted in the detoxification of  $H_2O_2$  generated in response to SA application. They also observed that antioxidant enzymes could protect the young leaves more than cotyledons and stems. Dat *et al.* [25] observed that the tobacco plants grown on an SA-supplemented medium had reduced activity of CAT, while GR, MDHAR, and DHAR activity enhanced, although APX was not significantly affected. The glutathione redox ratio GSH/(GSH+GSSG) was maintained despite increased GSH and GSSG levels. Along with this, the  $H_2O_2$  accumulation suggests changes in antioxidant enzyme activities that contributed to SA-induced thermotolerance.

SA transiently increased APX and lowered CAT but did not affect SOD and peroxidase (POX) in creeping bentgrass [43]. On the other hand, suggestions also prevail regarding the involvement of SA in scavenging active oxygen species (AOS) under heat stress as it increases the activities of CAT and SOD [48]. It also suppressed the  $O_2^-$  generation rate and decreased  $H_2O_2$  content significantly. SA (1 mM) effectively induced the activities of CAT, SOD, APX, and NADPH oxidase [49]. The  $H_2O_2$  accumulated in germinating seeds caused by SA had no association with CAT or APX inhibition. ROS induced by SA serves a role in plant stress-signaling [40]. They also found that the effect of SA on antioxidant enzymes was complex as SA treatment in the form of foliar spray increased SOD, CAT & DHAR activity.

Induced heat-stress tolerance response of 100  $\mu$ M foliar sprayed SA-pretreated *Cicer arietinum* seedlings was directly related to the coordinated response of antioxidative enzymes where POX and APX activities were increased, and CAT activity was decreased [50]. In contrast, when supplied with the nutrient solution, it increased SOD activity while the activities of CAT and DHA decreased. Wang and Li [44] reported the induced activities of APX, GR, and MDHAR and increased GSH/GSSG and ASA/DHA (reduced/oxidized ascorbate) ratio. The actions of APX, CAT and SOD were raised by the foliar spray of SA during grain filling in wheat, under both the heat stress and the recovery period [41]. This suggests a more effective operation of the Halliwell–Asada pathway and excess energy dissipation. It was recommended by Khanna *et al.* [45] that when SA is applied as a foliar spray to maize seedlings under heat stress, it starts a differential response of antioxidants through the Halliwell–Asada pathway. They reported

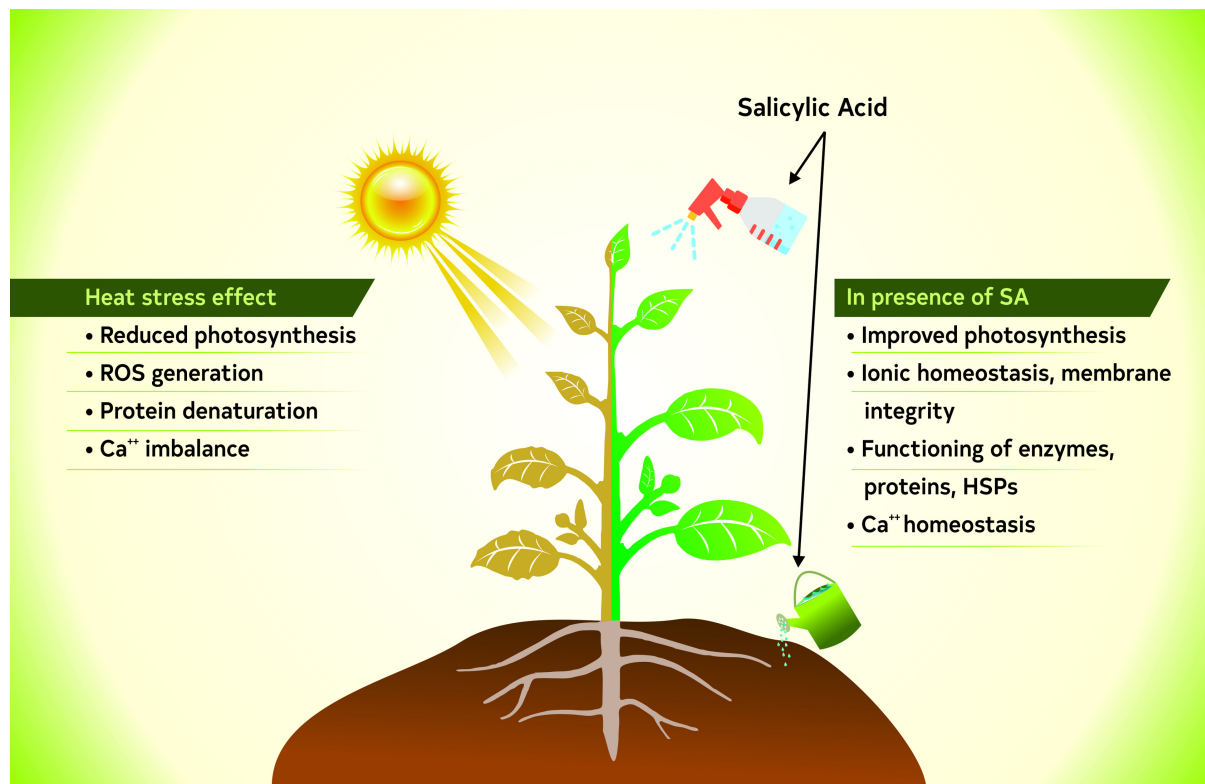


Fig. 3. Effects of heat stress and salicylic acid application in plants.

that heat-tolerant (CML-32) spring maize seedlings had increased activities of APX and GR in their roots and induced high POX activities in both the roots and shoots, whereas heat-sensitive (LM-11) spring maize seedlings had increased SOD and APX activity while GR remained unaffected in the shoots. Haydari *et al.* [51] observed an increase in the activity of antioxidant enzymes [SOD, CAT, glutathione S-transferase (GST), POX] had a positive effect on *Mentha arvensis* and *Mentha*  $\times$  *Piperita* plants. In addition, ascorbate content increased on the sixth day of the seedling growth (DSG) stage, which may be related to its enhanced biosynthesis under oxidative stress [100], which in turn would have resulted in substrate-induced APX activity activation.

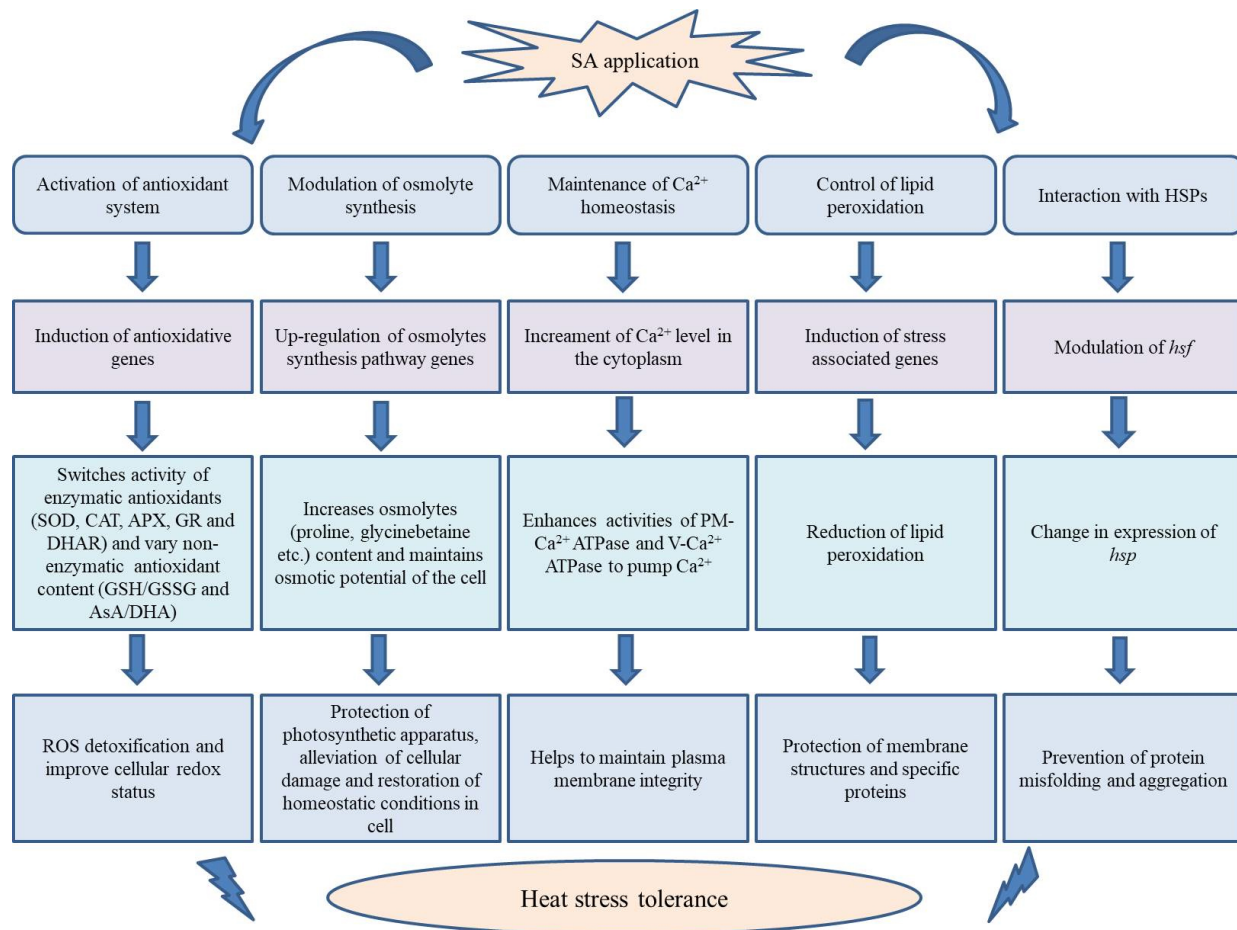
## 7. Interaction of SA with Osmolytes

Among the stress survival adaptive mechanisms, the accumulation of osmolytes like proline is worth discussing [101]. Plants evolved this mechanism to adapt to osmotic and ionic stresses and aid in the turgor maintenance in stressed plants [102]. Under stressful environments, proline biosynthesis via glutamate and pyrroline-5-carboxylate is enhanced in chloroplasts [103]. Proline regulates cellular osmotic homeostasis, safeguards biological membranes, stabilizes enzymes and proteins, and detoxifies excess ROS [104]. SA serves as a signaling molecule by inducing stress-associated genes, which generate osmolytes like proline, ultimately enhancing thermotolerance in plants [105]. In

this regard, Chakraborty and Tongden [50] observed significantly higher proline content in SA-treated *Cicer arietinum* seedlings than heat acclimatized seedlings. High proline accumulation is indicative of enhanced tolerance to heat-induced oxidative damage. SA (0.5 mM) treatment to heat-stressed wheat plants increased  $\gamma$ -glutamyl kinase activity and decreased proline oxidase activity, resulting in proline accumulation [31]. It acts as an antioxidant by increasing the osmotic potential, enabling plants to enhance water intake to maintain water balance. This has an important impact on stomatal aperture and photosynthetic machinery, which results in higher efficiency of PS II and increases Rubisco activity, ultimately protecting the photosynthetic apparatus from ROS. The proline content of heat-exposed spring maize seedlings increased after treatment with SA inferring that increased proline content helps improve the antioxidant response to high-temperature stress [45]. The proline content was significantly low under heat shock alone, while it increased when 1.0 mM SA was given along heat shock [52]. The heat-stressed SA-treated wheat plants had maximum free proline content [53]. A schematic representation of the potential mechanism underlying SA-conveyed plant heat stress tolerance (Figs. 3,4).

## 8. Maintenance of $\text{Ca}^{2+}$ Homeostasis by SA

Studying signal transduction during plant response and adaptation to stress is fascinating. During the most recent three decades, broad scope of extracellular signals



**Fig. 4. A potential mechanism underlying SA-conveyed plant heat stress tolerance.**

to specific responses has been elucidated, including  $\text{Ca}^{2+}$  functions as an intracellular messenger [106]. In plants,  $\text{Ca}^{2+}$  concentration in the cytoplasm ranges from 100 to 200 nM, while, in intracellular spaces and organelles, the limit reaches millimolar units [107]. Despite a significant electrochemical gradient for  $\text{Ca}^{2+}$  entrance into the cytoplasm, plant cells maintain a low amount of cytoplasmic  $\text{Ca}^{2+}$ . The transient rise in cytosolic free  $\text{Ca}^{2+}$  level occurs in response to the broad scope of the extracellular flag, such as heat stress [108]. To attain resting level  $\text{Ca}^{2+}$  and maintain  $\text{Ca}^{2+}$  homeostasis, the active pumping of  $\text{Ca}^{2+}$  to the apoplast or organelles is required [109]. Wang and Li [44] evidenced the involvement of  $\text{Ca}^{2+}$  in SA-induced heat tolerance. They illustrated that the SA-treated mesophyll cells of young grape plants possessed a higher cytosolic  $\text{Ca}^{2+}$  than that at an average temperature (27/18 °C day/night). After heat stress, this increased cytosolic  $\text{Ca}^{2+}$  returned to vacuoles or intracellular spaces, preventing chloroplast structure destruction. This suggests that increased  $\text{Ca}^{2+}$  in the cytoplasm due to SA pretreatment may help maintain the integrity of the plasma membrane to improve the tolerance to stress. Also, they showed that SA-treated leaves had higher activities of the plasma membrane (PM)- $\text{Ca}^{2+}$  ATPase and vacuolar (V)- $\text{Ca}^{2+}$  ATPase than controls which

enabled active pumping of  $\text{Ca}^{2+}$ . This signifies that SA can maintain  $\text{Ca}^{2+}$  homeostasis in the leaves under heat stress.  $\text{Ca}^{2+}$  plays a vital role, but still, Research is at the juvenile stage to establish a strong connection between  $\text{Ca}^{2+}$  mediated SA-induced thermotolerance.

## 9. Conclusions and Future Prospects

Heat stress adversely affects almost all plants' vegetative and reproductive health. Mitigation of the negative impact of heat stress involves applying various plant growth regulators/chemical agents. However, in recent times, salicylic acid gained a popular place in heat stress mitigation strategies. The crucial role of salicylic acid in plant growth and development is the main factor behind the popularity of SA as an 'effective therapeutic agent' for plants growing under diverse environmental conditions. It performs multiple roles, as evident by different studies conducted to understand its mechanism of action. Literature appraised herein confirmed the role of SA in protecting the plants from heat by modifying various physiological/biochemical processes. Its application improves the efficiency of almost every mechanism crucial for a plant's survival under heat, i.e., reproductive system, especially pollen health, HSPs production, which are involved in mitigation signal-

ing throughout the plant system, photosynthetic machinery, antioxidative system to relieve the stress, osmolytes and calcium metabolism which improves chemical homeostasis of the plant cells.

It should be noted that the specifics of the mechanisms that alleviate heat stress and the relationship between various aspects of SA in plant immunity and abiotic stresses are unknown. The area is still an open challenge at both the physiological and molecular levels. Further, extensive genomics and proteomics studies must reveal SA-responsive genes and proteins expressed upon exposure to stress. The complex mechanisms involving SA in producing and signaling specific plant metabolites and their influence on SA-endogenous levels can be unraveled by genomic and metabolomic approaches. The perception, transduction, and retrieval of knowledge regarding SA targets during signaling in the presence of heat stress remain ambiguous. It can be discovered using a multidisciplinary approach that includes genetics, molecular biology, biochemistry, genomics, metabolomics, bioinformatics, and computational biology.

An adequate understanding of its regulatory mechanism is indispensable to encourage future use. Various studies have presented SA as a capable and budding tool in mitigating the adverse effects of abiotic stress in plants. SA is maximally provided as a foliar spray. The development of its nanostructures such as nanoparticles, nanoformulations, nano-conjugates, or nano-encapsulation can be done to have better penetration efficiency at specific sites in the plant system. This innovative delivery system could allow the slow and constant release of the active component. Since SA application and its possible outcomes are highly dependent on the dose/amount applied, it is a fact that higher SA concentration doesn't profit plants. Therefore, additional research into the heat stress-regulated SA-catabolism process may be worthwhile to exploit SA as a potential phytoprotectant molecule. Another exciting area of study is to understand ecological implications related to SA application to plants as well as studying its signaling mechanism through the angle of ecology and evolution. These potential studies indicate several prospects for creating approaches that can improve overall sustainability in agricultural production systems through effective and productive management of abiotic and biotic problems posed by climate change.

## Abbreviations

ABA, Absciscic acid; ACS, 1-amino cyclopropane carboxylic acid synthase; AOS, Active oxygen species; APX, Ascorbate peroxidase; ASA, Acetylsalicylic acid; AsA, Ascorbate reduced; ATP, Adenosine triphosphate;  $\text{Ca}^{2+}$ , Calcium ion; CAT, Catalase; DAG, Diacylglycerol; DHA, Dehydroascorbate (Ascorbate oxidized); DHAR, Dehydroascorbatereductase; DREB, Drought responsive element binding protein; DSG, Day of seedling growth;

ETR, Electron transfer rate of PSII;  $F_j$ , Fluorescence intensity at 2 ms (the J-step);  $F_k$ , Fluorescence intensity at 300  $\mu\text{s}$ ;  $F_m$ , Maximum fluorescence;  $F_o$ , Initial fluorescence;  $F_v$ , Variable fluorescence;  $F_v/F_m$ ,  $(F_m - F_o)/F_m$  (maximum photochemical efficiency);  $F_v/F_o$ ,  $(F_m - F_o)/F_o$  (potential photochemical efficiency); GR, Glutathione reductase; GSH, Glutathione reduced; GSSG, Glutathione oxidized; GST, Glutathione S-transferase;  $\text{H}_2\text{O}_2$ , Hydrogen peroxide; HSF, Heat shock factors; HSP, Heat shock protein;  $\text{IP}_3$ , Inositol triphosphate; MDA, Malondialdehyde; MDHA, Monodehydroascorbate; MDHAR, Monodehydroascorbatereductase; mRNA, Messenger Ribonucleic acid;  $\text{NADP}^+$ , Nicotinamide adenine dinucleotide phosphate (oxidized); NADPH, Nicotinamide adenine dinucleotide phosphate (reduced); NPQ, Non-photochemical quenching;  $\text{O}_2^{\cdot-}$ , Superoxide anion; OEC, Oxygen evolving complex; P5C, Pyrroline-5-carboxylate; PAL, Phenylalanine ammonia-lyase;  $\text{PIP}_2$ , Phosphatidyl inositol 4,5-bisphosphate; PLC,  $\text{PIP}_2$ -phospholipase C; PMC, Pollen mother cell;  $P_n$ , Net photosynthesis rate; POX, Peroxidase\*; PSI, Photosystem I; PSII, Photosystem II; ROS, Reactive oxygen species; SA, Salicylic acid; SOD, Superoxide dismutase; SSS, Soluble starch synthase; TBARS, Thiobarbituric acid reactive substances;  $W_k$ ,  $(F_k - F_o)/(F_j - F_o)$ ;  $\phi\text{PSII}$ , Quantum yield of PSII electron transport;  $\psi\text{EO}$ , probability (at time 0) that a trapped exciton moves an electron into the electron transport chain beyond  $Q_A^-$ ;  $(1 - V_i)/(1 - V_j)$ , expression for redox state of PSI.

## Author Contributions

Conceptualization and supervision—SY, HSJ, JAP; Writing—SS (Sonali Sangwan), NS, HT, SS (Sushma Sharma); Writing-Review and editing—SY, JAP, PP, HP, RZS; Formal analysis—PP, WHA, RZS; Fund acquisition—PP, WHA. All authors contributed to editorial changes in the manuscript. All authors read and approved the final manuscript.

## Ethics Approval and Consent to Participate

Not applicable.

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## Conflict of Interest

The authors declare no conflict of interest.

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