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REVIEW

Revolutionizing High Temperature Stress Relief: Exploring the Latest Advances in Salicylic Acid Application

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Abstract

In the context of climate change, high-temperature stress poses a significant threat to plant growth and crop productivity. Due to the rise in global temperature, it is necessary to understand and manage the harmful effects of heat stress (HS) on plants. Salicylic acid (SA) is a naturally existing phytohormone. It plays an important role in boosting the ability of plants to withstand different environmental stresses, such as high temperature. This review delves into the various roles of SA to mitigate the harmful effects of HS in plants. SA, known for its traditional function in plant defense mechanisms against pathogens, has been identified as a regulator of numerous physiological, biochemical and molecular processes. SA mitigates high temperature stress (HTS) through diverse mechanisms, encompassing the control of antioxidant systems, adjustment of heat shock protein (HSPs) expression, preservation of membrane stability and induction of osmoprotectants. Furthermore, this review discusses the practical applications of SA in agriculture to enhance crop heat tolerance. External application of SA or SA analogs has exhibited promising results in improving crop yield and quality under HS conditions. However, the precise mechanisms of SA-mediated thermotolerance in different plant species and genotypes require further investigation. In conclusion, SA emerges as a vital regulator in the complex network of plant responses to HTS, requires further exploration of molecular and biochemical mechanisms by which SA improves plant thermotolerance.

Keywords Osmoprotectants · Photosynthesis · Salicylic acid · Stress · Thermotolerance

Abbreviations

ABA	Abscisic acid
APX	Ascorbate peroxidase
CAT	Catalase
GB	Glycine betaine
GPX	Glutathione peroxidase
GST	Glutathione-S-transferase
HS	Heat stress
HSPs	Heat shock proteins
HTS	High temperature stress
IAA	Indole acetic acid
POX	Peroxidase
ROS	Reactive oxygen species
SA	Salicylic acid
SOD	Superoxide dismutase

Introduction

Plants confront various environmental challenges throughout their lifespan. Abiotic stresses such as extreme temperatures, drought, salinity and exposure to toxic metal ions can significantly affect plant health and performance (Oshunsanya et al. 2019). Due to climate change the frequency of extreme weather events has increased, thereby intensifying the harmful effects of abiotic stresses on plants (Zhao et al. 2020). Globally, there is a recognition that the increasing temperature pose a substantial threat to agricultural productivity (Myers et al. 2017). The fifth assessment report of the IPCC projected that the annual daily maximum temperature would increase by around 1–3 °C by the middle

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of the 21st century (Intergovernmental Panel on Climate Change [IPCC] 2014). As the global temperature continues to increase, it is very important to understand its consequences on agriculture, ecosystems and food security (Muluneh 2021).

High temperatures pose a risk to the photosynthetic machinery in plants, leading to reduced carbon dioxide uptake and ultimately diminished crop yields (Mondal et al. 2016). At elevated temperatures, plants respire more rapidly (Ferguson et al. 2021). Although respiration is crucial for energy production, excessive respiration can deplete the plant's energy reserves, resulting in fewer resources available for growth and reproduction. High temperatures can amplify water stress in plants by increasing the rate of evapotranspiration. This can lead to water loss through transpiration exceeding the plant's ability to absorb water from the soil, resulting in wilting, leaf damage and ultimately dehydration (Marchin et al. 2022). Elevated temperatures can exert widespread and adverse impacts on plant health, growth and reproductive processes (Parthasarathi et al. 2022).

To combat these challenges, certain plants utilize strategies like stomatal closure to reduce water loss and maintain cellular turgor and hydration. Additionally, plants may accumulate osmoprotectants like glycine betaine, proline and soluble sugars. These substances reduce the osmotic potential within cells, allowing the plant to retain water in adverse conditions (Sihag et al. 2024).

HTS leads to increase in ROS within plant cells (Liu et al. 2021). These ROS include reactive molecules and free radicals derived from molecular oxygen, all of these are known to cause damage to the cell membrane of plants (Demidchik and Shabala 2017). The increased production of ROS under HS conditions poses a considerable risk to cellular components and it disturbs various physiological processes occurring in plant cells (Ul Hassan et al. 2021). In response to oxidative stress, plant cells activate antioxidant defense systems to mitigate the negative effects of ROS and maintain cellular homeostasis (Dumanović et al. 2021). These defensive mechanisms include enzymes such as catalase (CAT), peroxidase (POX), ascorbate peroxidase (APX), superoxide dismutase (SOD), glutathione peroxidase (GPX), and glutathione S-transferase (GST) (Rajput et al. 2021). Numerous studies have shown that several high-molecular-weight heat shock proteins (HSPs) exhibit responses to increased temperature stress. These HSPs safeguard cell membranes by stabilizing membrane proteins and prevent lipid peroxidation (Khan and Shahwar 2020). HSPs play a crucial role in preserving the thermostability of cell membrane during HS (Hemantaranjan et al. 2014). Certain plants may modify the composition of their membrane lipids, synthesizing more heat-tolerant lipid molecules to improve membrane stability in response to HTS (Prasertthai et al. 2022).

Overall, these physiological processes are interconnected and collectively enhance a plant's capacity to tolerate HTS. The ability to regulate water balance, accumulate protective solutes, maintain photosynthesis and preserve cell membrane integrity are essential processes that enable plants to survive and adapt to challenging HS conditions. Figure 1 illustrates the effects of HTS on morphological, biochemical, physiological and yield parameters in plants. Plant species and genotypes with greater tolerance to high temperatures often exhibit enhanced capabilities in these processes.

In response to HS conditions, plants activate a complex network of interconnected signaling pathways which allow them to reduce the harmful effects of elevated temperature (Li et al. 2021). In challenging environments, the coordination between phytohormone signaling pathways and metabolites becomes essential for regulating plant growth and development. This cooperation plays a central role in

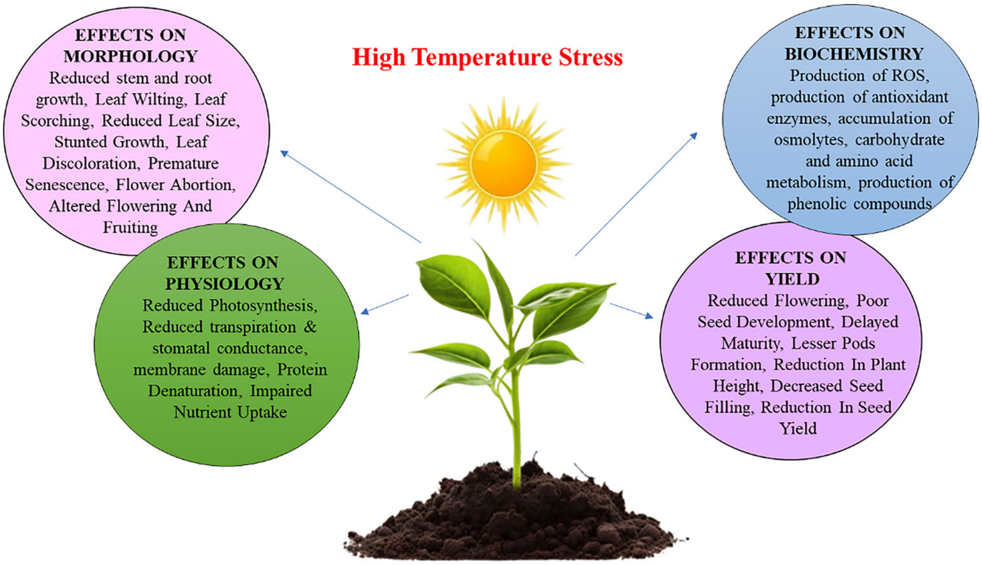

Fig. 1 Effects of heat stress on morphology, physiology, biochemistry and yield of plants

Table 1 A list of research findings on the role of SA in regulating HS responses in plants

Crops	Concentration of SA Treatment	Mode of application	Observation recorded	References
Agrostis stolonifera	10 µmol L^{-1}	Foliar spray	Increase in antioxidant enzymes activity and photosynthetic rate	(Larkindale and Huang 2004)
Nicotiana tabacum	70 µM	Protoplast incubation	Upregulated the expression of Hsp 70	(Cronjé et al. 2004)
Cucumis sativa L	1 mM	Foliar spray	Decrease in electrolyte leakage, H_2O_2 and thiobarbituric acid reactive substances (TBARS). Enhanced maximum yield of photosystem II photochemical reactions (Fv/Fm), the quantum yield of the photosystem II electron transport (ΦPSII) and antioxidant enzymes	(Shi et al. 2006)
Brassica juncea L	10^{-5} M	Foliar spray	Antioxidant enzymes and level of proline significantly increased	(Hayat et al. 2009)
Cicer arietinum	1, 1.5 and 2 mM	Foliar spray	Higher induction of POD and PPO activities, higher accumulation of phenols, H_2O_2 and proteins	(War et al. 2011)
Triticum aestivum L	0.5 mM	Foliar spray	Increase in proline metabolism, N assimilation and photosynthesis	(Khan et al. 2013)
Sorghum **bicolor**	362 µM	Seed Priming	Increase in germination, seedling growth and antioxidant system and decrease in MDA content was observed	(Nimir et al. 2015)
Oryza sativa L	1 and 10 mmol L^{-1}	Foliar spray	Increase in grain yield, spikelet number per panicle, setting rate and antioxidant enzymes	(Zhang et al. 2017)
Triticum aestivum	10^{-4} M	Foliar spray and Seed Priming	Increase in sugars, protein, proline, chlorophyll and yield parameters	(Munir and Shabbir 2018)
Oryza sativa L	0.01, 0.1, 1.0, 10 and 50 mM	Foliar spray	Higher pollen viability measurement, increase in H_2O_2 content, antioxidant enzymes and decrease in MDA content was observed	(Feng et al. 2018)
Solanum lycopersicum L	1 mM	Foliar spray	Enhanced the gas exchange parameters, quantum yield of photosystem II (Fv/Fm), water use efficiency, reduced electrolyte leakage and increased the antioxidant enzymes activity	(Jahan et al. 2019)
Oryza sativa L	100 mg L^{-1}	Foliar spray	Increase in total soluble sugars, fresh, dry weight, root and shoot lengths, potassium, phosphorous, magnesium nitrate, nitrite reductase, protein content and nitrogen	(Akasha et al. 2019)
Physalis peruviana L	150 mM	Foliar spray	Increase in proline content, H_2O_2 content, superoxide dismutase activity and decrease in catalase activity was observed	(Şahin 2019)
Euphorbia pulcherrima	200 and 400 µM	Foliar spray	Decrease in MDA content, Electrolyte leakage and increase in antioxidant enzymes	(Lin et al. 2019)
Medicago sativa L	0.25 and 0.5 mM	Foliar spray	Increase in chlorophyll content, plant height, biomass, photosynthetic efficiency and decrease in electrolyte leakage, MDA content	(Wassie et al. 2020)
Capsicum annuum L	0.5 mM	Foliar spray	Increase in spermine, spermidine concentrations and ion concentrations	(Otálora et al. 2020)
Salvia officinalis L. *and Salviaelegans Vahl*	100, 200, 400 and 800 µM	Foliar spray	Increase in normalized difference vegetation index, Soil-plant analysis development and Fv/Fm	(Lin et al. 2021)
Triticum aestivum	0.1 mmol	Foliar spray	Increase in Fv/Fm, leaf area, photochemical efficiency (ΦPSII), activity of sucrose phosphate synthase (SPS)	(Fan et al. 2022)

sensing and adapting to abiotic stress in plants (Rasool et al. 2018).

Various phytohormones, such as auxin, cytokinins, abscisic acid, gibberellic acid, brassinosteroids, nitric oxide, salicylic acid and polyamines, play crucial roles in mitigating the effects of HS on plant growth and development (Lubovská et al. 2014). Phytohormones regulates vital physiological processes during both normal growth phases and stress conditions in plants (Fahad et al. 2015). Consequently, considerable attention has been focused on investigating the external application of phytohormones to enhance stress tolerance. The literature contains numerous studies for enhancement of thermotolerance through external applications of phytohormones. For example, IAA and ABA not only initiate signal transduction pathways but also regulate the growth and quality of Kentucky bluegrass under HS conditions (Li et al. 2014). In *Arabidopsis*, the non-protein amino acid β-aminobutyric acid (BABA) has been found to augment acquired high-temperature tolerance, potentially by modulating the ABA (Zimmerli et al. 2008). The participation of brassinosteroids in plant responses to HTS has been observed (Zhang et al. 2013). Ethylene and cytokinins have been identified as mediators of HS signals in plants (Sagar et al. 2021). The alleviation of HTS in plants is significantly facilitated by SA, which triggers a range of physiological, biochemical and molecular responses (Kaya et al. 2023). The review extensively examines various aspects, including the interplay of SA with the photosynthetic machinery, heat shock proteins, changes in antioxidants, lipid peroxidation, accumulation of crucial osmolytes like proline, glycine betaine and the impact on membrane stability, reproduction, phenology and yield of plants.

Role of Salicylic Acid in High Temperature Stress Tolerance

SA, a naturally occurring phytohormone, has traditionally been associated with plant defense against pathogens. However, recent research has shown that it also contributes to enhancing plant thermotolerance (Sangwan et al. 2022). Exogenous application of SA initiates mechanisms of abiotic stress tolerance in plants under various stress conditions (Song et al. 2023). The impact of SA on plants depends on its dosage, with both low and high concentrations leading to different results for the same plant species (Wani et al. 2017). The optimal concentration for SA treatment varies based on parameters such as treatment duration, plant type, plant age and the specific part of the plant being treated (Lawlor and Paul 2014). A concise summary of multiple studies investigating the mitigation of heat stress through the application of SA is given in Table 1.

Effect of Heat Stress On Membrane Injury Indices and Its Mitigation Through SA Application

The application of salicylic acid (SA) has been shown to enhance membrane stability during heat stress, reducing the adverse effects associated with ROS production. SA foliar treatment has been reported to decrease ion leakage and lipid peroxidation in alfalfa subjected to HTS, suggesting its role in improving membrane stability under stress conditions (Wassie et al. 2020). In fenugreek seedlings exposed to a high temperature of 40 °C, the application of SA led to a remarkable reduction in heat injury by 60% compared to seedlings subjected to heat stress alone (Choudhary et al. 2024). This protective effect of SA is attributed to its ability to modulate the plant's antioxidant defense system, which reduces oxidative stress and maintains cellular homeostasis. In wheat, SA significantly enhanced growth by decreasing the accumulation of malondialdehyde (MDA), hydrogen peroxide (H_2O_2), and electrolyte leakage (Alsahli et al. 2019). Under HS conditions, plants treated with a foliar spray of SA exhibited lower levels of MDA, indicating enhanced membrane integrity. Consequently, these plants showed better growth compared to those without SA treatment (Younis et al. 2021).

Role of Salicylic Acid in Antioxidant Metabolism Under High Temperature Stress

Salicylic acid (SA) plays a critical role in enhancing the antioxidant defense mechanisms of plants, particularly under high-temperature stress (HTS). The external application of SA has been shown to regulate the activity of antioxidative enzymes, thereby bolstering a plant's ability to withstand abiotic stresses (Parashar et al. 2014). Research indicates that the application of SA significantly increases the activity of key antioxidant enzymes, which helps mitigate oxidative damage caused by HTS. In rice plants, cultivated under ideal temperature conditions, only minimal elevations in the activities of antioxidant enzymes are observed. Conversely, when rice plants are exposed to high temperatures and treated with SA, there is a significant enhancement in the action of antioxidant enzymes (Ahmed et al. 2024). Similarly, the pretreatment with SA increases the survival rate of maize seedlings under high-temperature conditions. This improvement is accompanied by enhanced accumulation of osmolytes and activation of the antioxidant system, demonstrating SA's protective effects (Li et al. 2015).

Further studies illustrate SA's role in stress mitigation across various plant species. In *Ulva prolifera*, SA alleviates the heat stress-induced upregulation of antioxidant-related proteins and enzymes (Fan et al. 2017). In *Digitalis tro-*

jana, pretreatment with SA improves tolerance to HTS by increasing the activities of SOD and CAT in callus cultures (Cingoz and Gurel 2016). In ornamental pepper seedlings, treatment with SA significantly boosts the activity of CAT, SOD, and POD, along with increasing the content of ascorbic acid (ASA) and glutathione (GSH) in seedlings exposed to HTS (Zhang et al. 2020). Additionally, in *bell pepper*, SA and epibrassinolide (EBR) treatments increased the activity of various antioxidant enzymes, aiding in the scavenging of ROS generated due to elevated temperatures (Preet et al. 2023). An elevation in CAT and SOD activity is also observed in SA-treated tomato plants under heat stress (Jahan et al. 2019). In potato plants, the activity of APX increases in heat-stressed plants following foliar application of SA (Li et al. 2019).

Quantitative studies further illustrate the antioxidative benefits of SA. In pigeon pea genotypes at the seedling stage, the antioxidative defense system shows a marked increase in enzyme activity following SA treatment. CAT activity shows an average 1.02-fold rise in heat-acclimated plants, a 0.77-fold increase in those treated with 0.5 mM SA, and a 1-fold increase in those treated with 1 mM SA. Similarly, POX activity exhibits an average 1.30-fold increase in heat-acclimated plants, a 1.24-fold increase in those treated with 0.5 mM SA, and a 1.37-fold increase in those treated with 1 mM SA (Kaur et al. 2019). The application of SA emerges as a promising strategy for enhancing plant resilience to high-temperature stress. By activating antioxidant enzyme systems and increasing osmolyte accumulation, SA helps plants maintain cellular homeostasis and mitigate oxidative damage. This highlights the potential of SA as a valuable tool in agricultural practices aimed at improving crop tolerance to abiotic stresses.

Interaction of SA with Osmolytes

In response to high temperatures, plants employ various strategies, one of which involves the synthesis of low molecular weight water-soluble compounds referred to as compatible solutes. These include proline, proteins, glycine betaine, carbohydrates and polyols. When plants experience heat stress, the accumulation of these osmolytes serves several purposes: aiding in osmotic balance, elevating the concentration of cell protoplasm to uphold membrane function and adjusting the antioxidant system to restore cellular redox balance and overall homeostasis (Kaur and Asthir 2015). Proline accumulation in plants serves as a protective mechanism against osmotic stress induced by high temperatures. As a compatible solute, proline protects the cell from the adverse effects of heat stress. Iqbal et al. (2014) observed an elevation in proline content under HTS. This elevation in proline level regulates osmotic balance, preserves membrane integrity and detoxifies excessive reactive oxygen species (ROS).

In rice, HTS led to a significant increase in proline levels by 45.5% compared to control plants. This rise can be attributed to increased proline synthesis and reduced catabolism processes during heat exposure (Gautam et al. 2022). Similarly, Pareek et al. (2019) noted an elevation in proline accumulation in chickpea during the initial stages of heat exposure, suggesting that proline accumulation serves as a mechanism to preserve RWC, thereby protecting plants from damage and sustaining normal cellular hydration levels. According to Khan et al. (2015), salicylic acid plays a regulatory role in controlling the synthesis of osmolytes and other metabolites, as well as in managing the nutritional status of plants. In cucumber, Basirat and Mousavi (2022) discovered that SA reduces dehydration losses by triggering an antioxidant defense mechanism and boosting the accumulation of proline.

Pirnajmedin et al. (2020) studied the impact of SA on the induction of high-temperature tolerance in fescue genotypes under field conditions. Their findings revealed that the foliar application of SA resulted in a significant increase in proline content compared to the control. According to Nazar et al. (2011), methionine synthesized from homocysteine through the sulfur (S) assimilation pathway activated by SA plays a pivotal role in the production of GB. According to Quan et al. (2022), the accumulation of glycine betaine (GB) significantly mitigates the effects of high-temperature stress in Brassica. GB not only alleviates the reduction in photosynthesis and the excessive accumulation of ROS but also activates stress-responsive genes under high-temperature conditions. GB serves to stabilize photosynthesis in plants experiencing heat stress, thereby promoting growth even under challenging thermal conditions. Additionally, it plays a crucial role in preventing photoinhibition by stabilizing the structure of the oxygen-evolving center, particularly within photosystem II (PSII) (Brengi and Nasef 2023).

Khan et al. (2014) showed that SA enhances GB accumulation and suppresses ethylene formation in mung bean, resulting in improved photosynthesis and growth. SA-induced elevations in osmolyte concentration may establish an intracellular redox state that is favorable for optimal metabolic and physiological activities during stressful conditions (Dawood et al. 2020).

Influence of SA On the Synthesis of Heat Shock Proteins During High Temperature Stress

To endure high temperatures, plants activate heat-resistant strategies, which involve altering organelles and cytoskeleton arrangement, adjusting membrane flexibility and boosting levels of antioxidant enzymes alongside generating protective molecules like antioxidants (Goud et al. 2022). The heat-shock response is a crucial mechanism in plants that triggers the rapid production HSPs when exposed to high temperature (Doyle et al. 2013). During severe HS, many proteins within the chloroplast experience denaturation. HSPs act as molecular chaperones, protecting these proteins and preserving their structural integrity and function (Goswami et al. 2021). HSPs consists of five principal classes of proteins i.e. HSP100, HSP90, HSP70, HSP60 and small HSPs (Zhao et al. 2018). The rapid expression of HSP genes is controlled by heat-shock factors (HSFs), which are transcription factors that form trimers in response to stress conditions, move into the cell nucleus and initiate the transcription of HSPs (Jacob et al. 2017). Vidya et al. (2018) noted that a majority of HSPs, such as HSP28, HSP26.5 and HSP22, were activated during the initial phases of HS. HSP27 is significantly induced as a HSP in response to various stress conditions, particularly HS (Das and Bhattacharya 2017). A heat shock protein, 'CsHSP45.9' enhanced tolerance to HS by activating the antioxidant system (Kim et al. 2020). Yang et al. (2020) conducted a study on the overexpression of sHSP17.6 and its effect on mitigating the inhibited growth and development caused by HS in *Arabidopsis thaliana.* Both control and SA-treated grapevine leaves exhibited an increase in HSP21 during HS. After stressed plants recover, the synthesis of HSPs stops and they were degraded. However, under control conditions, the levels of HSP21 decreased during the recovery phase (Wang et al. 2010). SA heightened the expression of hsp17, with higher expression observed in the thermotolerant (C 306) wheat variety compared to the thermosensitive (PBW 343) variety (Kumar et al. 2015). These proteins possess protein refolding capabilities, thereby enhancing the thermotolerance of the plants. After application exogenous SA (0.1 mM) increase in production of HSP70 and HSP17.6 in pea plants was observed (Pan et al. 2006). Similarly, Rai et al. (2020) noted an upregulated expression of heat shock transcription factor (hsf) in *Lablab purpureus* under HS. This upregulation of HSF might be due to activation of protein kinases after SA application. These are further involved in the refolding and transport of antioxidant proteins to the mitochondria.

Influence of SA On the Photosynthetic Apparatus Under High Temperature Stress

It is well known that photosynthesis is extremely vulnerable to elevated temperature. HS disrupts the delicate balance of cellular energy processes (Mathur et al. 2014). It deactivates heat-sensitive proteins like rubisco activase and downregulates essential chloroplast components. This results in reduced photosynthetic efficiency, redox imbalance and cell death (Li et al. 2018). High temperatures primarily impact photochemical reactions within the thylakoid lamellae and carbon metabolism within the stroma of chloroplasts. Among the protein complexes within the chloroplast thylakoid membrane, PSII stands out as particularly susceptible to HTS. Severe heat-induced damage to PSII critically impairs photosynthetic electron transport and ATP synthesis (Wang et al. 2018). High temperatures led to a decrease in the maximal photochemical efficiency (Fv/Fm) and caused damage to PSII in tobacco leaves (Yanhui et al. 2020). Similar outcomes were recorded by in chickpea under HS (Jha et al. 2022). According to Zhou et al. 2015, the decrease in the Fv/Fm value was noted due to damage of D1 reaction-center protein of PS II under HTS conditions. The decline in carotenoid and chlorophyll content observed in *Lablab purpureus* plants under elevated temperature can be linked to several factors. Firstly, osmotic stress resulting from reduced RWC and limited CO_2 availability may lead to the oxidation of chlorophyll and other pigments. This oxidative stress can trigger the generation of excess ROS within chloroplasts. Additionally, stomatal closure induced by high temperatures further exacerbates this process, contributing to the decrease in pigment content (Rai et al. 2017). Research indicates that SA primarily acts to safeguard chloroplasts within the photosynthetic system during periods of HS (Janda et al. 2014). SA maintain the stability of photosynthetic pigments and supports the functioning of photosystems such as PSI and PSII. Additionally, it ensures that plants can effectively carry out carbon assimilation, enabling normal growth without disruption. Applying SA before exposure to high temperatures mitigated the decline in photosynthetic capacity of the flag leaves. Consequently, this pre-application ensured the stability of the photosynthetic system despite the presence of HS (Fan et al. 2022). SA had a beneficial effect in maintaining a high level of photosynthetic capacity in ornamental pepper seedlings when exposed to higher temperature (Zhang et al. 2020). Applying SA to the foliage prior to HS helped in alleviating oxidative damage in *Solanum lycopersicum.* This was achieved by enhancing photosynthetic function and increasing the activity of antioxidant system. As a result, scavenging of ROS was increased, which safeguarded the photosynthetic apparatus and facilitated plant survival in stressful conditions (Jahan et al. 2019). HS significantly impairs the growth, physiological functions and photosynthetic activity of alfalfa. Nevertheless, pretreating alfalfa with exogenous SA notably improved all growth parameters, physiological processes and photosynthetic activity. This enhancement led to increased heat tolerance, with particularly notable effects observed at a low concentration of SA (0.25 mM) (Wassie et al. 2020). Applying SA during

HS resulted in elevated production of proline. This increase in proline maintained osmotic balance of the plants, enabling them to absorb more water. As a result, functioning of the photosynthetic machinery was improved. This enhanced PS II efficiency and activity of Rubisco, ultimately increase in photosynthetic rate was observed (Khan et al. 2013; Waqas et al. 2021; Wang et al. 2010). When maize plants treated with SA were subjected to HTS, they showed fewer reductions in the number of lamellae per grana and less noticeable alterations in the structure of their chloroplasts. These findings suggest that SA optimizes photosynthetic carbon assimilation and activates the antioxidant system. This treatment may mitigate the adverse effects of photoinhibition in PSII and reduce structural damage to chloroplasts (Li et al. 2023).

Role of SA in Protecting Plant Reproductive Systems During High Temperature Stress

It has been observed that the reproductive stage of many crops is particularly vulnerable and can only withstand a narrow temperature range (Lohani et al. 2020). The economic significance of cultivated plant species lies in the success of their sexual phase, namely seed or fruit production. When temperatures during flowering exceed the species tolerance range, it adversely affects fruit and seed set (Chaudhary et al. 2022). HTS has detrimental effects on the reproductive structures. It may lead to abnormalities in both male and female gametes (Resentini et al. 2023). Sexual reproduction in flowering plants consists of various stages, each differing in their susceptibility to HS (Fig. 2).

Plant sexual reproduction relies on the development of viable pollen in anthers. The process of conversion of anthers to pollen grains is affected by severe stress conditions, particularly during meiosis and the young microspore stage, where even brief exposure can significantly reduce pollen fertility. This is primarily due to disruptions in tapetum

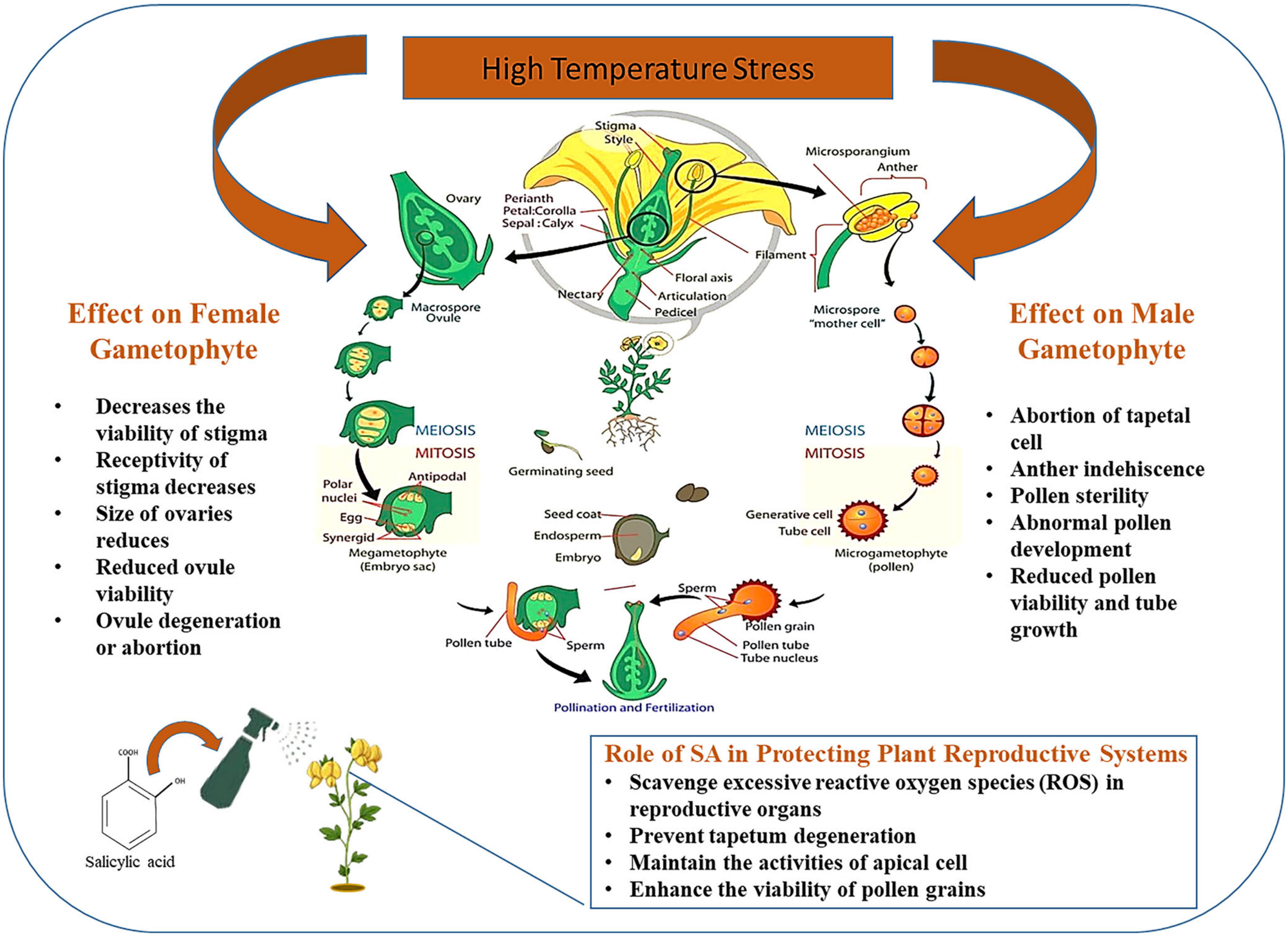

Fig. 2 The Influence of high temperature stress on plant reproductive systems and the protective role of salicylic acid

development and degradation, ultimately resulting in the production of abnormal pollen (Ye et al. 2010; Niu et al. 2013).

Studies have indicated that the young microspore stage is particularly sensitive to high temperatures (Draeger and Moore 2017). HS during this phase leads to the microspores degeneration and the enlargement of tapetal cells, ultimately resulting in male sterility (Smith and Zhao 2016; Deng et al. 2016). Elevated temperatures reduced pollen activity as a result of improper development of PMC and premature tapetum degradation. Consequently, this led to improper fertilization and decrease grain number in panicles (Liu et al. 2020). Consistent exposure to HS during the reproductive phase leads to sterility in *Cucumis sativus* L. (Chen et al. 2021). To investigate this phenomenon, researchers conducted a cross-sectional analysis of anther development under HTS. Their observations revealed abnormalities in tapetum and microspore in stressed anthers. Furthermore, they observed increase in pollen abortion and a significant decline in pollen fertility. Increase in pollen viability and seed-setting rates were reported after SA application in rice plants during HS conditions. This positive effect was mainly attributed to SA's capacity to reduce excessive levels of ROS in anthers, thereby preventing tapetum degradation induced by HTS (Feng et al. 2018). Research in rice suggests that SA plays a crucial role in preventing pollen abortion and enhancing crop yield under HS conditions (Zhang et al. 2017). SA foliar spray significantly improved pollen viability, resulting in a higher percentage of filled grains in rice (Ahmed et al. 2024). Low concentration of SA improved pollen viability under HS conditions by enhancing jasmonic acid signaling in developing anthers (Jansma et al. 2022). In Arabidopsis, SA alters the activities of apical cells, indicating its involvement in the processes of flowering and pollen tip growth. (Rong et al. 2016).

Effect of High Temperature Stress On the Phenology and Yield of Crops and Its Mitigation Trough SA Application

The duration from sowing to maturity plays a crucial role in determining the overall yield of plants (Chauhan and Williams 2018). Mungbean plants exhibit up to a 46% reduction in flower count and a 15–45% reduction in pod set during high-temperature stress (HS) conditions (Sharma et al. 2022). HS can lead to early phenological events, accompanied by shortened durations of both the flowering and podding stages (Malaviarachchi et al. 2016). Temperatures exceeding the critical threshold during rice growth stages reduce both quality and grain yield (Jagadish et al. 2015). Late sowing can lead to an overall reduction in phenological development, affecting the duration of the vegetative phase, flowering and podding stages (Maphosa et al. 2023).

Salicylic acid (SA) has been shown to promote flowering and fruit set in plants, demonstrating its beneficial effects not only under normal growth conditions but also in stressful environments (Pacheco et al. 2013). Similar outcomes have also been reported in alfalfa, where SA application improved plant response to stress (Wassie et al. 2020). Foliar application of SA stimulated flowering and increased pod number in soybean plants (Sukumar et al. 2015). The application of exogenous SA significantly enhanced wheat yield when subjected to high-temperature conditions. In particular, pre-application of SA during the anthesis stage proved most effective in mitigating the detrimental effects of HS on wheat yield during the grain-filling stage (Fan et al. 2022). Application of SA to wheat plants at a concentration of 150 mM significantly increased both yield and yield-related characteristics (Chouhan et al. 2017). Furthermore, acetyl salicylic acid has been found to improve both vegetative and reproductive growth, coupled with an increase in the number of leaves, flowers and total yield in tomato plants (Shinwari et al. 2018). These findings underscore the potential of SA as a strategic application to improve plant resilience and productivity under high-temperature stress conditions.

Conclusion and Future Prospects

The latest studies highlights a significant loss in global crop production due to HS. This condition negatively impacts the growth, development and productivity of plants. Increased temperatures disturb both the physiological and molecular processes within plants. SA is recognized as a powerful therapeutic agent for plants adapting to various environmental conditions. SA controls the expression of HSP, initiates the production of various antioxidants and osmoprotectants and influences metabolic pathways and processes in plants. Its effectiveness is underscored by numerous studies aimed at understanding its mechanism of action and revealing its diverse contributions to maintaining plant health. A visual representation (Fig. 3) elucidates the diverse functions of SA in response to elevated temperature. SA maintains membrane stability, photosynthetic machinery, enhance the antioxidative system to alleviate stress, regulates osmolytes, synthesizing various HSPs crucial for signaling throughout the plant system. Together, these actions contribute to maintaining chemical homeostasis in plant cells. Understanding the precise mechanisms that mitigate high-temperature stress is crucial and this remains a persistent challenge at both physiological and molecular levels. Additionally, the exact mechanisms and pathways for the actions of SA in plants are not fully understood. To address this knowledge

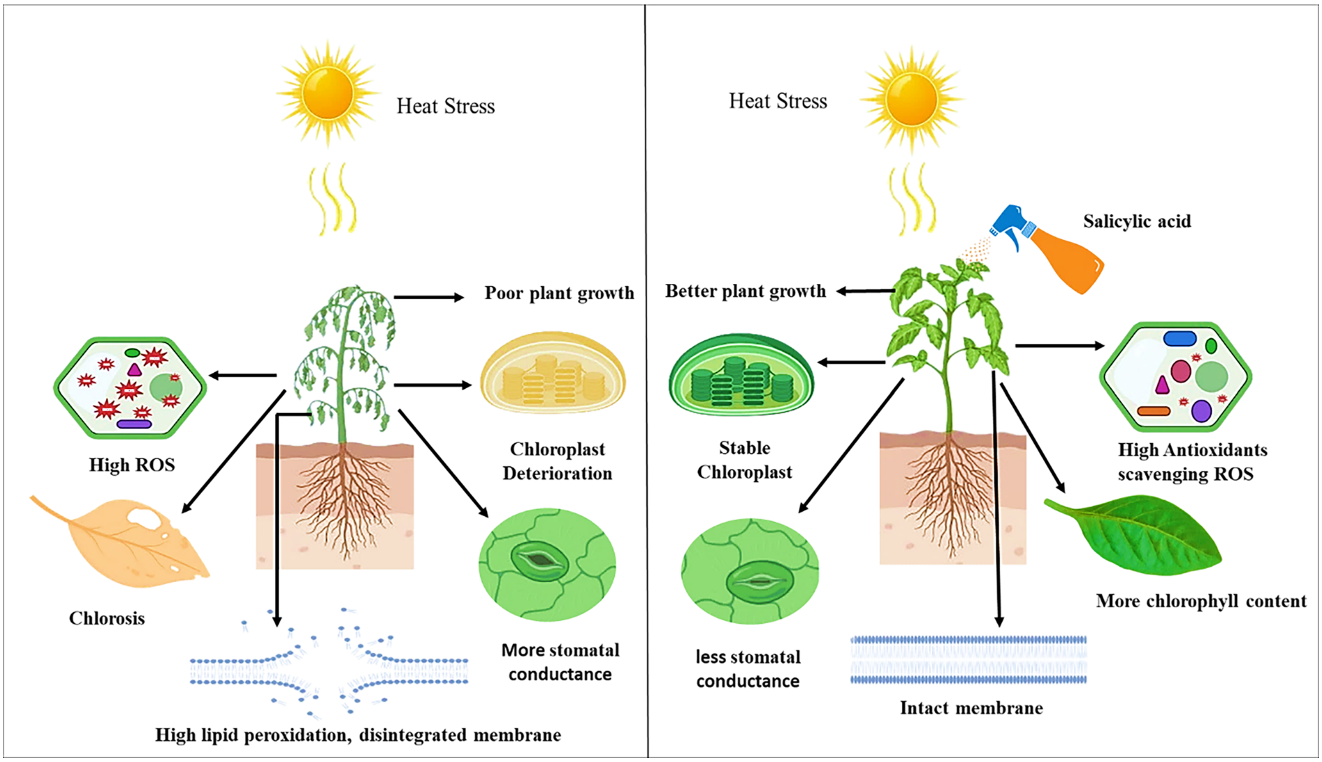

Fig. 3 The effects of high temperature on plants and its relief through the use of salicylic acid application

gap, comprehensive genomics and proteomics studies are essential to identify the genes for SA regulation and proteins expressed under stress conditions. Further research is required to elucidate the interaction between phytohormones and heat stress tolerance. This is vital for the advancement of genotypes with improved tolerance to high temperatures.

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Conflict of interest M. Janaagal, P. Sharma, G. Kumari, H. Gulia, G. Suresh, S. Tallapragada, S. Devi, N. Lakra, S.S. Arya and P. Pooja declare that they have no competing interests.

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