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Role of Salicylic Acid in Mitigating Stress and Improving Productivity of Crops: A Review

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

Plant stress encompasses the alterations occurring in plants when confronted with adverse environmental conditions. These conditions, though not immediately life-threatening, trigger alarm signals within the plants. Stress can arise from two primary factors: abiotic stress, such as drought, heat, or salinity, and biotic stress, caused by pathogens like insects, viruses, or bacteria. Plant growth regulators (PGRs) serve as an effective method to assist plants in coping with stress. Salicylic acid (SA), a crucial PGR, regulates various facets of plant growth and development. It influences seed germination, organ development, stomatal movement, photoperiodic responses, and aging. SA aids plants in combating environmental stressors like cold, heat, drought, and salinity, while also bolstering defenses against diseases. External application of SA becomes necessary when the natural levels in plants are insufficient to manage stress. SA can be derived from willow bark, extracted from plants like mango or broccoli, or synthesized from phenylalanine or phenol. Its application during stress conditions triggers protective antioxidant responses, enhances nutrient uptake under salinity, aids photosynthesis and metabolite movement in heat stress, and promotes root development and resilience to waterlogging. SA's interactions with other PGRs like auxin, ethylene, and abscisic acid further assist plants in tolerating multiple stressors. Although research has explored SA's role in mitigating individual stresses, further investigation is needed, particularly in real-world field conditions where plants face concurrent stressors.

Keywords: Edge computing; serverless architectures; cloud computing; big data management; scalability, sustainability; operational costs*; latency reduction.*

ABBREVIATION

IAA : Indole-3-Acetic Acid
CK : Cytokinins
GA : Gibberellins
ABA : Abscisic Acid
ET : Ethylene
JA : Jasmonic Acid
SA : Salicylic Acid
BR : Brassinosteroids
IC : Isochorismate
SA-Asp : Salicyloyl-Aspartic Acid
PAL : Phenylalanine Ammonia-Lyase Pathway
SAG : Salicylic Acid 2-O-β-Glucoside
ICS : Isochorismate Synthase
SGE : Salicyloyl Glucose Ester
BA2H : Benzoic Acid-2-Hydroxylase
IPL : Isochorismate Pyruvate-Lyase Methyltransferase
MeSA : methylsalicylate
ROS : Reactive Oxygen Species
STP : Signal Transduction Pathway
SAR : Systemic Acquired Resistance
PRR : Pattern Recognition Receptors
PAMP : Pathogen-Associated Molecular Patterns
HR : Hypersensitive Response
ETI : Effector-Triggered Immunity

1. INTRODUCTION

Plant stress can be defined as any unfavorable condition or substance that hampers a plant's metabolic processes, growth, or development [1]. Plant stress is typically categorized into two main types: biotic stress, caused by factors like bacteria, viruses, fungi, and insects, and abiotic stress, stemming from environmental factors such as heat, drought, salinity, cold, waterlogging, and heavy metals. Abiotic stresses pose a significant threat to global agricultural productivity, with human activities contributing to the degradation of agricultural systems. It is projected that abiotic stresses could potentially reduce the yield of staple food crops by 70% and overall crop production by more than 50% [2]. Therefore, it is crucial to improve plant performance and mitigate the loss of productivity caused by abiotic stress. One approach to achieve this is through the exogenous application of plant hormones. Plant growth regulators (PGRs) are organic compounds used to stimulate, inhibit, or modify plant growth and development. PGRs act as signaling molecules and are effective in very low concentrations transmitting information throughout the plant [3-6]. These PGRs include Indole-3-Acetic acid (IAA), cytokinins (CK), gibberellins (GA), abscisic acid (ABA), ethylene (ET), jasmonic acid (JA), salicylic acid (SA), brassinosteroids (BR), and others, all playing essential roles in plant growth and development. PGRs are considered vital endogenous substances that regulate molecular and physiological responses, making them essential for the survival of plants as stationary life forms [7,8]. Salicylic acid ($C_7H_6O_3$) is a widely distributed plant growth regulator with positive effects on various plant growth and developmental processes. Research has shown its roles in seed germination, flowering, yield, ion uptake and transport, photosynthetic rate, induction of defense-related genes, and stress resistance in plants facing biotic stress. The importance of SA under abiotic stress conditions is undeniable [9]. It is a naturally occurring plant hormone belonging to the group of phenolic acids and is primarily produced within the plant's cytoplasmic cells.

2. ROLE OF SALICYLIC ACID IN PLANTS

- Enhances physiological processes and the efficient translocation of photosynthates toward reproductive organs, improving yield and productivity.
- Promotes plant growth and development, as well as ion uptake and transport.
- Stimulates cell division and differentiation, accelerating the formation of photosynthetic pigments and delaying leaf aging.
- Minimizes both biotic and abiotic stresses.

3. FUNCTION OF SALICYLIC ACID IN PLANTS UNDER STRESS CONDITION

Salicylic acid provides a broader range of tolerance to various abiotic stresses such as drought, salt, cold, heat, and heavy metals. It also plays a role in various plant developmental processes, including root elongation, trichome development, stamen development, and leaf senescence [10]. Serving as signaling molecules, SAs regulate the expression of numerous genes in response to abiotic stresses and promote specific protective mechanisms. The crucial role of SA in plant stress tolerance and adaptation has been extensively documented

4. SOURCES OF SALICYLIC ACID

Salicylic acid can be sourced from various places. It is naturally isolated from the bark of willow trees (*Salix* spp.), which contains salicin at levels of 9.5-11%. SA is found in the plant in the form of free phenolic acids or associated with amino compounds. Willow tree bark is particularly rich in SA and can be found near marshes and in sunny areas. It is native to China. It can also be synthesized, either through the biosynthesis of the amino acid phenylalanine or from phenol. Additionally, it can be extracted from natural sources like mango, broccoli, cauliflower, and tomatoes. Salicylic acid is available in both liquid and solid formulations.

5. SALICYLIC ACID BIOSYNTHESIS AND METABOLISM

The biosynthesis and metabolism of salicylic acid (SA) involve intricate pathways, with two prominent routes being the isochorismate (IC) pathway and the phenylalanine ammonia-lyase (PAL) pathway. Both of these pathways originate from chorismic acid, which is the end product derived from the shikimic acid pathway in the plastids [11]. The conversion of chorismic acid to IC is catalyzed by isochorismate synthase (ICS), a reaction reported in several plant species [12]. Isochorismate pyruvate lyase (IPL) is believed to facilitate the transformation of IC into SA.

Once synthesized, SA can undergo various modifications. Glucosylation of SA results in the formation of salicyloyl glucose ester (SGE) and salicylic acid 2-O-β-glucoside (SAG), a process involving the activity of UDP-glucosyltransferase [13]. SAG can be stored in the plant's vacuole, contributing to SA's regulation. Additionally, SA can be methylated by SAM-dependent carboxyl methyl transferase to produce methyl salicylate (MeSA) [14]. MeSA, once produced, can be transported to different parts of the plant, serving various roles in intra- and inter-plant signaling.

The production and metabolism of SA represent a dynamic and intricately regulated system in plants, with multiple pathways and modifications that impact the plant's responses to both biotic and abiotic stresses. Understanding these processes is critical for harnessing the potential benefits of SA in enhancing plant health and stress resilience.

When plants experience various abiotic stresses such as drought, cold, heat, salinity, heavy metal exposure, and other stressors, they exhibit an increase in reactive oxygen species (ROS) activity, a decrease in photosynthetic activity, and reduced plant growth and development. This ultimately leads to decreased crop yield and productivity. The fine equilibrium between ROS production and ROS elimination is disrupted by different stressors like salinity, drought, extreme temperatures, heavy metals, pollution, pathogen infections, and more. Consequently, the survival of plants hinges on several crucial factors, including alterations in growth conditions, the severity and duration of stress, and the plants' ability to rapidly adapt to changing energy dynamics [15]. Reactive oxygen species (ROS) primarily consist of singlet oxygen (O_2), Hydrogen Peroxide (H_2O_2), Superoxide (O_2^-), and hydroxyl radicals (OH-). Salicylic acid is the most extensively researched phytohormone in terms of its involvement in managing oxidative stress. It has been demonstrated to be highly efficient in detoxifying ROS within plant cells due to its numerous effects.

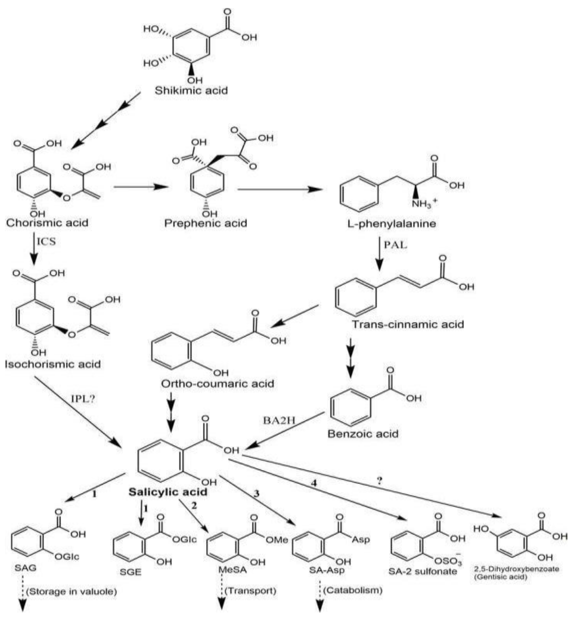

Fig. 1. Proposed pathways for Salicylic acid biosynthesis and metabolism

IC: Isochorismate, SA-Asp: Salicyloyl-Aspartic Acid, PAL: Phenylalanine Ammonia-Lyase Pathway, SAG: Salicylic Acid 2-O-β-Glucoside, ICS: Isochorismate Synthase, SGE: Salicyloyl Glucose Ester, BA2H: Benzoic Acid-2-Hydroxylase, IPL: Isochorismate Pyruvate-Lyase Methyltransferase, MeSA: Methylsalicylate, 1: UDP-Glucosyltransferase, 2: SAM-Dependent Carboxyl, 3: GH3-Like Phytohormone Amino Acid Syntethasesalicylic acid and 4: Sulfotransferase

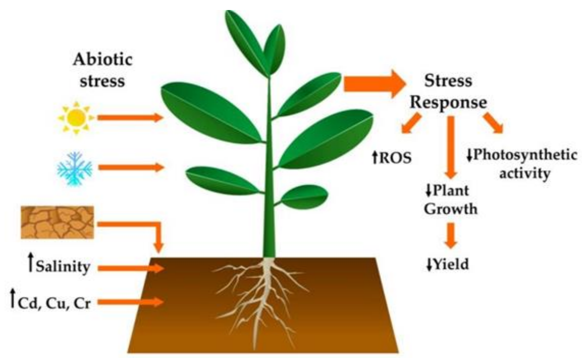

Fig. 2. Effects of abiotic stresses on crop productivity and quality of the produce

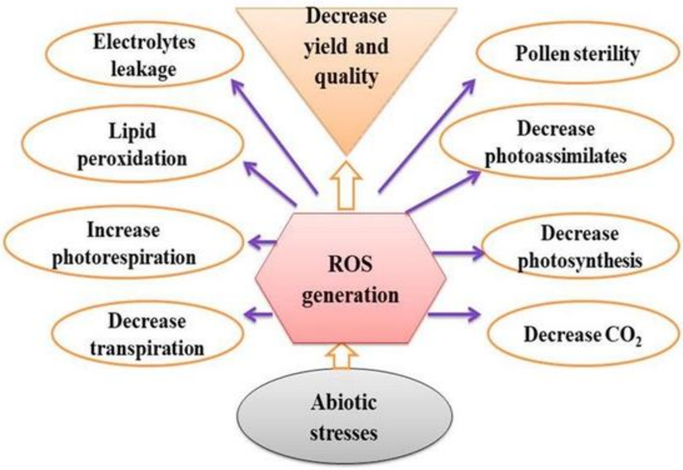

Fig. 3. Effects of ROS generation on plant productivity and quality of the produce

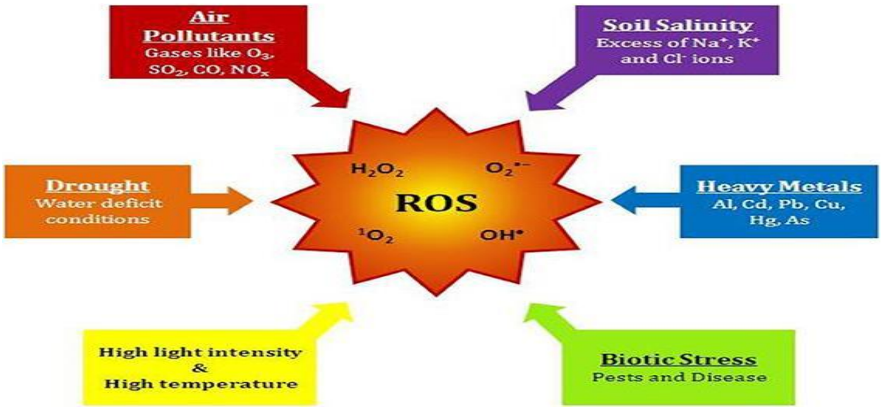

Fig. 4. Various causes responsible for ROS generation

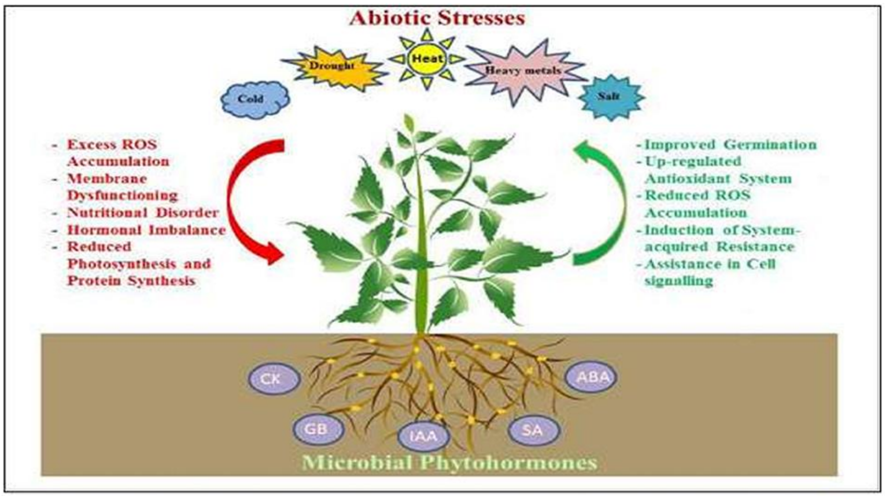

Fig. 5. A schematic diagram of the abiotic stress-induced disorders in plants and the involvement of Salicylic acid in plant tolerance to various abiotic stresses

Many microbes associated with plant roots produce cytokinin (CK), gibberellin (GB), Indole-3-Acetic acid (IAA), salicylic acid (SA), and abscisic acid (ABA). These compounds aid plants in coping with stress by enhancing their antioxidant capabilities, increasing the expression of the antioxidant system, and accumulating compatible osmolytes. This reduces damage caused by oxidative stress, enhances photosynthetic efficiency and membrane stability, encourages cell division and regulates stomatal function, promotes root system growth, and facilitates the acquisition of water and nutrients [16].

6. ALLEVIATING ABIOTIC STRESSES: PROMINENCE OF SALICYLIC ACID

The role of salicylic acid (SA) as a phytohormone in governing plant growth and development is well-established. Over the past few years, extensive research has been conducted on the potential of SA in alleviating abiotic stress. Numerous research findings have shown that the external application of SA enhances a plant's ability to withstand adverse conditions such as salinity, drought, extreme temperatures, and heavy metal exposure.

6.1 Drought Stress

Drought stress is a primary factor contributing to reduced crop production and even crop failure. Typically, it negatively impacts plant growth, photosynthetic rates, and leads to leaf wilting. Moreover, drought stress triggers oxidative reactions, membrane lipid peroxidation, and the production of antioxidant enzymes. Cellular dehydration, osmotic stress, and the generation of reactive oxygen species (ROS) result from water loss in plant cells during drought stress. One of the major constraints on plant growth is the damage inflicted by ROS on biological macromolecules. The application of SA to plant leaves can improve their tolerance to water stress, reduce water loss by regulating stomatal aperture, and enhance growth characteristics, yield, and yield-related attributes. In the field experiment, investigated the impact of salicylic acid (SA) on Indian mustard productivity [17]. The study featured three treatments: a control group (T1), SA application at 100 ppm during flowering and siliqua formation (T2), and SA application at 200 ppm at the same stages (T3). All treatments received a uniform application of recommended N, P2O5, K2O, and Sulfur. SA was dissolved in ethanol and applied as a foliar spray. The results revealed that SA at 200 ppm significantly improved plant height, dry matter per plant, siliquae per plant, seed yield, stover yield, and oil yield, comparable to the other treatments. Study reported in rainfed lentil study, seed priming with 200 ppm salicylic acid yielded the best results, increasing plant height and the number of branches [18]. These findings align with previous research indicating SA's role in enhancing plant growth and branching [19].

6.2 Salinity Stress

Salinity stress is a global issue that significantly impedes plant growth, reduces yields, and negatively affects seedling vigor and root development. This stress condition disrupts plant metabolism, causing nutrient deficiencies, membrane abnormalities, and genetic damage. Furthermore, it retards plant growth due to both ionic toxicity (resulting from sodium ions, Na+, and chloride ions, Cl-) and osmotic effects. Additionally, salinity stress can trigger oxidative stress by elevating the production of reactive oxygen species, including free radicals, hydrogen peroxide (H_2O_2), and singlet oxygen. A Study documented that salicylic acid (SA) reduces the uptake of sodium by plants while enhancing the absorption of essential nutrients such as nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) in comparison to control treatments during periods of salt stress [20]. Consequently, both naturally occurring and externally applied SA can augment a plant's ability to tolerate salt stress. In a study conducted in Egypt, it was observed that sunflower plants were grown on saline-affected soil during the summer season [21]. The experiment examined the effects of different salicylic acid rates and soil salinity levels on sunflower plant growth and yield. Results showed that higher soil salinity reduced plant growth and yield, while increased salicylic acid application, particularly at 1.4 mM, significantly enhanced plant performance under varying levels of soil salinity. Similarly, in other experiment, the impact of foliar application of salicylic acid on mung bean growth under salt stress was investigated [22]. The study used two mung bean varieties and different salt concentrations. Salinity led to increased ROS levels and Na+ ion accumulation, negatively affecting photosynthetic pigments, water content, growth, and yield. However, foliar spray with 100 ppm salicylic acid significantly improved all growth and yield parameters compared to the control.

6.3 Heat Stress

In order to meet the growing needs of the rapidly expanding global population, agriculture relies heavily on achieving high plant yields and economic biomass production. High-temperature stress poses a critical challenge for all major agricultural crops, potentially resulting in reduced yields. This stress adversely impacts the physiological processes in plants, disrupting cellular balance, interactions between plants, soil, and water, as well as photosynthesis and respiration. It also leads to damage to cell membranes and the development of leaf chlorosis and necrosis, ultimately reducing both plant biomass and yield. Salicylic acid (SA) plays a pivotal role in enhancing photosynthesis, facilitating the active movement of metabolites, and improving nutrient uptake. As a result, it contributes to increased crop yield and overall productivity. In other field experiment the impact of salicylic acid (SA) on wheat yield was studied [23]. The research, using a split-plot design with three replications, tested four SA levels (Control, SA 50 ppm, SA 100 ppm, and SA 150 ppm) applied at 50 and 80 days after sowing. The findings revealed that SA at 150 ppm effectively countered the adverse effects of high temperature on wheat yield and related traits, offering promising results for wheat genotypes.

6.4 Waterlogging Stress

Waterlogging is a prominent abiotic stress that affects plants by impeding aerobic respiration. This condition results from decreased oxygen levels in the soil, which in turn hinders the growth and development of crops, often resulting in significant yield losses or even crop failure. Waterlogging induces oxidative stress in plants due to the accumulation of reactive oxygen species (ROS), leading to damage in the lipid membrane. However, through the external application of salicylic acid (SA), crops can effectively mitigate the adverse effects of waterlogging stress. This is because SA plays a crucial role in the development of the root system and aerenchyma, enabling crops to withstand waterlogging stress. In a pot experiment at Banaras Hindu University where the researchers examined the impact of salicylic acid (SA) on the H-86 (Kashi Vishesh) variety of tomato plants under waterlogged conditions in a poly house [24]. Tomato seedlings were pre-treated with SA (50 ppm and 100 ppm) before transplantation. Waterlogging stress was applied for 12 hours at 15 and 45 days after transplanting, and SA was foliar-sprayed at different growth stages. Morphological and biochemical traits were recorded.

6.5 Heavy Metal Stress

Heavy metals are metallic chemical elements with high density that can be toxic at low concentrations. These substances have a direct or indirect impact on photosynthesis and can significantly inhibit plant growth and development. They also disrupt metabolic processes, leading to issues such as membrane damage, activation or inhibition of enzyme activity, and DNA damage. Salicylic acid (SA) alleviates oxidative stress and indirectly reduces the uptake of metals from the growth medium by activating the antioxidant systems in plants. Among phytohormones, SA serves as a versatile growth regulator with the capacity to modulate various physiological and metabolic processes. It plays a vital role in plants' defense mechanisms against heavy metal toxicity [25]. Previous research has demonstrated that applying SA to leaves enhances resistance to various heavy metal stress conditions in different crops, such as lead stress in rice and barley [26], and cadmium stress in maize. Exogenous SA application helps maintain the cell membrane's stability and integrity, boosts antioxidant activity by reducing reactive oxygen species (ROS), enhances photosynthetic capacity, and reduces the uptake of heavy metals [27]. In a Dhaka pot experiment was conducted where the researchers investigated the effect of foliar-applied salicylic acid (SA) on Brassica campestris plants in lead-amended soils [28]. Lead treatments were applied, and SA at 0.25 mM was used to counter Pb-induced stress. Pb stress led to increased ROS levels and oxidative damage in mustard plants. SA application improved growth, yield attributes, and final yield by enhancing the antioxidant defense system, thus increasing stress resistance and productivity.

6.6 Cold Stress

Low temperatures represent a significant constraint on plant growth and development, greatly influencing the geographic range of plants. There are two primary forms of low-temperature stress: chilling and freezing stress, which occur at temperatures above and below 0°C, respectively, and can result in plant injury. Plants have evolved intricate mechanisms to tolerate these stress factors, involving the activation of hormone-related genes and the accumulation of cold-induced stress-related proteins, amino acids, and soluble sugars to mitigate subsequent cell membrane damage. Under normal cold stress conditions, changes in

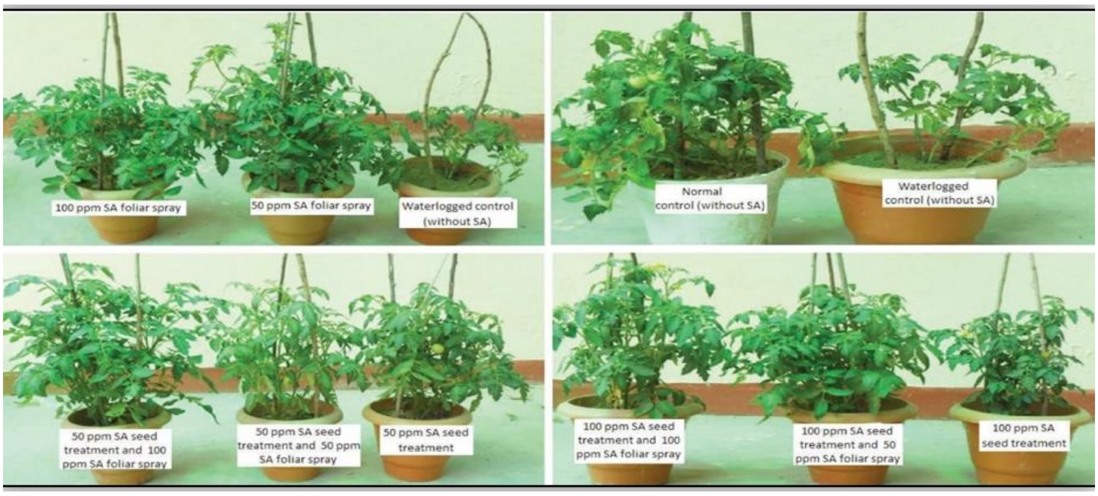

Fig. 6. Effect of different concentrations of salicylic acid (SA) on tomato plants under waterlogging stress

cytoplasm viscosity, enzyme activities, and the development of chlorosis, necrosis, and membrane damage occur in plant cells. Moreover, it disrupts plant processes and cellular machinery, upsetting cell balance. The application of exogenous salicylic acid (SA) enhances a plant's ability to endure freezing temperatures, improves photosynthesis capacity, reinforces antioxidant defenses, and aids in osmotic adjustment under low-temperature conditions. Consequently, it effectively mitigates the adverse effects of cold stress on plant growth, development, and grain yield. The influence of exogenous salicylic acid (SA) on wheat plants under low-temperature conditions was examined using a field air temperature control system [29,30]. SA pre-treatment effectively mitigated the adverse effects of low temperatures on plant height, biomass, and grain yield. Low-temperature stress reduced photosynthesis and overall plant growth, leading to decreased grain yield. The study revealed that SA pre-treatment, particularly SL (SA pretreatment + low-temperature treatment), outperformed the control, highlighting the effectiveness of exogenous SA in enhancing wheat's resilience to late spring low-temperature stress in the field.

7. SALICYLIC ACID AND BIOTIC STRESS CONDITION

Biotic stress in plants results from the actions of pathogens and insects. When a pathogen interacts with the plant's plasma membrane, it initiates a Signal Transduction Pathway (STP). This STP, in turn, triggers a Hypersensitive Response (HR) characterized by the formation of a yellow halo due to the production of phytoalexins. Phytoalexins are small antimicrobial molecules that eliminate nearby infected cells. Prior to their demise, these cells release Salicylic Acid (SA), which is then transported throughout the plant to prevent further infection. This defensive reaction is known as Systemic Acquired Resistance (SAR). Effector-Triggered Immunity (ETI) is an integral component of the plant's innate immune system, serving as the primary defense mechanism against pathogens. Plants employ Pattern Recognition Receptors (PRR) to identify conserved microbial cues. Infected cells directly detect the pathogen attack through recognition of Pathogen-Associated Molecular Patterns (PAMPs), prompting the activation of an immune response.

8. RELATIONSHIP BETWEEN SALICYLIC ACID AND OTHER PHYTOHORMONES

The relationship between salicylic acid (SA) and other phytohormones in plants is a highly intricate and tightly regulated system that influences various aspects of plant growth, development, and responses to environmental stressors [31]. These interactions are essential for the overall well-being and adaptability of plants. Here, we'll elaborate on how SA interacts with key phytohormones:

8.1 Auxin

SA and auxin often have antagonistic effects. While auxin promotes cell elongation and division, SA can inhibit these processes. This antagonistic interaction can help plants balance growth and defense responses, particularly during pathogen attacks.

8.2 Ethylene

SA and ethylene often have antagonistic effects as well. Ethylene is involved in stress responses and senescence, and SA can mitigate some of these ethylene-induced effects. However, they can also act synergistically in certain stress situations.

8.3 Abscisic Acid (ABA)

SA and ABA can have both positive and negative interactions. ABA is generally involved in stress responses and stomatal regulation. The balance between these two hormones is crucial for a plant's response to environmental stresses. SA can both enhance and suppress ABA responses, depending on the context.

8.4 Gibberellic Acid (GA)

SA and GA interactions are often antagonistic. GA promotes growth and development, while SA can suppress these processes. During stress situations, SA's presence can lead to reduced levels of GA and thereby prioritize defense mechanisms over growths.

8.5 Jasmonic Acid (JA)

SA and JA have a complex relationship. They are often antagonistic but can also act synergistically in certain cases. JA is primarily associated with defense responses against herbivores and necrotrophic pathogens, while SA is more related to biotrophic pathogens. The balance between these two hormones is essential for tailoring the plant's response to specific stressors.

These interactions involve intricate signaling pathways and crosstalk mechanisms that enable plants to fine-tune their responses to different stressors. The outcome of these interactions can vary depending on the type of stress and the specific plant species involved. For instance, during a biotrophic pathogen attack, SA often accumulates to activate defense responses, while ethylene and jasmonic acid may be suppressed to prioritize resistance over growth. Conversely, during abiotic stress, such as drought or salinity, the balance between ABA and SA becomes crucial for regulating stomatal closure, conserving water, and minimizing damage.

9. CONCLUSION

Salicylic acid (SA) has emerged as a compelling focus of research due to its multifaceted roles in plant biology. It operates as both a developmental regulator and a crucial player in defense signaling mechanisms when plants confront an array of abiotic stressors. SA-induced modifications ripple through plant systems, profoundly impacting physiological, biochemical, and molecular pathways. One of the most striking findings across numerous studies is the capacity of SA to amplify the plant's antioxidant defenses, actively curbing the generation of reactive oxygen species (ROS), which are notorious culprits in stress-induced damage. This bolstered antioxidant activity enhances the plant's resilience against an assortment of abiotic stressors, ranging from the scorching heat of summer to the bone-chilling cold of winter, and even the harsh salt-laden soils of saline environments. The production of SA under these adverse conditions serves as a proactive shield, not only fortifying the plant's innate defenses but also inciting resistance against pests and insects. Nevertheless, delving into the intricacies of plant responses to SA and environmental stress necessitates innovative approaches and tools. The complexities of plant hormone systems and the sheer volume of data accumulated present challenges in the precise control of SA during environmental stress. Nevertheless, unraveling the intricacies of SA's signal transduction mechanisms in response to a spectrum of environmental stressors holds great promise for the future. This understanding could substantially bolster plant stress tolerance, potentially culminating in superior plant survival rates and elevated agricultural yields, a prospect of immense significance in the ongoing quest for sustainable agriculture amid a changing climate and increasing environmental pressures.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declares that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during writing or editing of manuscripts.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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