Efficacy of Salicylic Acid in Response to Plant Stress Tolerance, Growth and Productivity: A Review

Abstract

Plant stress generated by various climatic and anthropogenic activities has exacerbated the degradation of agricultural systems and productivity throughout the developmental era, and it is currently recognized as the world's most significant and possibly deadly danger impacting crop plant economic output. Nonetheless, phytohormones have been found as a potent tool for minimizing the detrimental effects of stressors in agricultural plants in a sustainable manner. Salicylic acid (SA), one of the most important phytohormones, is required for the regulation of plant growth, development, ripening, and defensive responses. A lot of interest has been generated by SA's defensive mechanism. Major agricultural crops' ability to withstand stress has been said to be much improved. SA utilization is influenced by the amount of SA applied, the application method, and the state of the plants (such as their developmental stage and level of acclimation). In this review, we have focus on the efficacy of SA on mitigating various plant biotic and abiotic stress under adverse environmental conditions and its role on plant growth, development and productivity.

Keywords: Salicylic acid, stress tolerance, defence mechanism, growth, development and productivity

Introduction

Current climate circumstances and anthropogenic activity are among the most damaging elements causing massive agricultural losses throughout the world. The aforementioned challenges, such as high temperatures, salinity, drought, and cold, are significant variables that limit agricultural output. With the environment being altered and rare natural resources being exploited more economically, the global agricultural goal of increasing food production by 70% by the year 2050 for approximately 2.3 billion new-born people is facing serious challenges (FAO, 2009). “Impact of climate change on ecosystems have had a serious negative influence on the gross agronomy, making these efforts ineffective” (Dimeyeva *et al.*, 2015). Crops are being subjected to an increase in stressors (biotic and abiotic stress) as a consequence of the impact of human activity and the intensification of climate change, which has become the main factor in the deterioration of agricultural systems and the loss in grain output (Sinha *et al*., 2021). As a result, developing plants to withstand or tolerate stressors (biotic and abiotic) using previously discovered resistance mechanisms will be part of the sustainable development approach. Salicylic acid (SA), for instance, has been shown to be crucial in resistance and defensive signaling under both biotic and saline stress (Verma *et al*., 2017).

"Salicylic acid (SA) is a naturally occurring small-molecule phenolic compounds that possesses an aromatic ring and a hydroxyl group. It functions as a signal sensor to control plant response. Through the control of procedures including antioxidant defense, nitrogen metabolism, photosynthesis, and water stress, it shields plant cells from the toxicity of ion buildup and cell death" (Peng *et al*., 2021). Because of its numerous physio-biochemical and developmental activities in hormonal interactions as well as its antioxidant characteristics, salicylic acid (SA), a common plant phenolic molecule, is an efficient stress reliever (Laishram *et al*., 2020). It has been shown to increase tolerance and defense against pathogen attack (Raskin *et al*., 1990), as well as to mitigate the harmful effects of several environmental stresses on plants, including low temperature and chilling (Korkmaz *et al*., 2007; Horvath *et al*., 2007), high temperature and drought (Senaratna *et al*., 2000), and salinity (Yildirim *et al*., 2008). Additionally, it improves seedling emergence and germination rates and percentages, ensuring adequate crop stand under a variety of environmental circumstances (Laishram *et al*., 2023).

Salicylic acid is regarded as a crucial signalling molecule that contributes to local and endemic disease resistance in plants as a result of diverse pathogenic assaults (Alverez, 2000). In addition to conferring disease resistance, SA may be able to regulate how plants respond to various oxidative stresses. Significant advancements have been achieved in pinpointing the essential elements and comprehending the functions of SA and nutrients connected to plant defense pathways. In this review, the multifunctional roles of salicylic acid in crops have been summarized and illustrated. These roles include defense mechanisms, tolerance to a variety of biotic and abiotic stresses, biosynthesis, signaling, effectiveness on bio-productivity, growth, activities of various enzymes in plants, as well as the necessary space constraints.

Salicylic acid (SA) biosynthesis pathway

The endogenously produced phytohormone SA (2-hydroxybenzoic acid) that is present in plants is a phenolic substance with a seven-carbon (C) backbone. Two primary secondary metabolite-producing pathways—the shikimic acid system and the malonic acid pathway—produce these plant phenolic compounds. However, the majority of phenolic compounds in plants are created via the shikimic acid system, which does so by converting aromatic amino acids, such as phenylalanine, which is the precursor of SA, into precursors of carbohydrates acquired through glycolysis and the pentose phosphate pathway. Although another system termed the isochorismate pathway also accumulates SA in plants, the phenylalanine pathway is responsible for producing the majority of the SA there is (Kawano *et al*., 2004; Mustafa *et al*., 2009). The phenylalanine ammonia-lyase (PAL) enzyme acts on the phenylalanine to remove ammonia, which results in the formation of trans-cinnamic acid in the phenylalanine pathway. Cinnamic acid serves as a precursor for two different chemicals, one of which is coumaric acid, which is created when an enzyme called cinnamate-4-hydroxylase (C_4H) hydroxylates cinnamic acid at the C4 position. The subsequent oxidation of its side chain and hydroxylation of coumaric acid lead to the production of SA. Cinnamic acid is converted into a second product, benzoic acid, which is then subjected to ortho-positional hydroxylation, which results in the creation of SA (Mustafa *et al*., 2009).

By virtue of the activity of the enzyme isochorismate synthase (ICS), chorismate serves as a precursor for isochorismate in the isochorismate pathway (Fig. 1). The enzyme isochorismate pyruvate lyase converts isochorismate into SA (Mustafa *et al*., 2009). The ICS level increases in plant cells in response to biotic or abiotic stressors, which results in a high level of SA in plant defense mechanisms (Wildermuth *et al*., 2001). The majority of the SA in plants still exists in its inactive, glycosylated form. The enzyme UDP-glucose SA-glucosyltransferase glycolyzes SA. However, SA glycosidase changes SA from its inert state into one that is active. These two enzymes also function as regulators, determining the degree of SA in plant cells under various environmental conditions. Arabidopsis under stress uses isochorismate to create SA mostly in chloroplasts. Other crops may have other pathways for producing SA. Under typical development conditions, rice accumulates significant amounts of SA, around tenfold higher than that of Arabidopsis leaves (Klessig *et al*., 2016). SA biosynthesis is carefully regulated during biotic and abiotic stress.

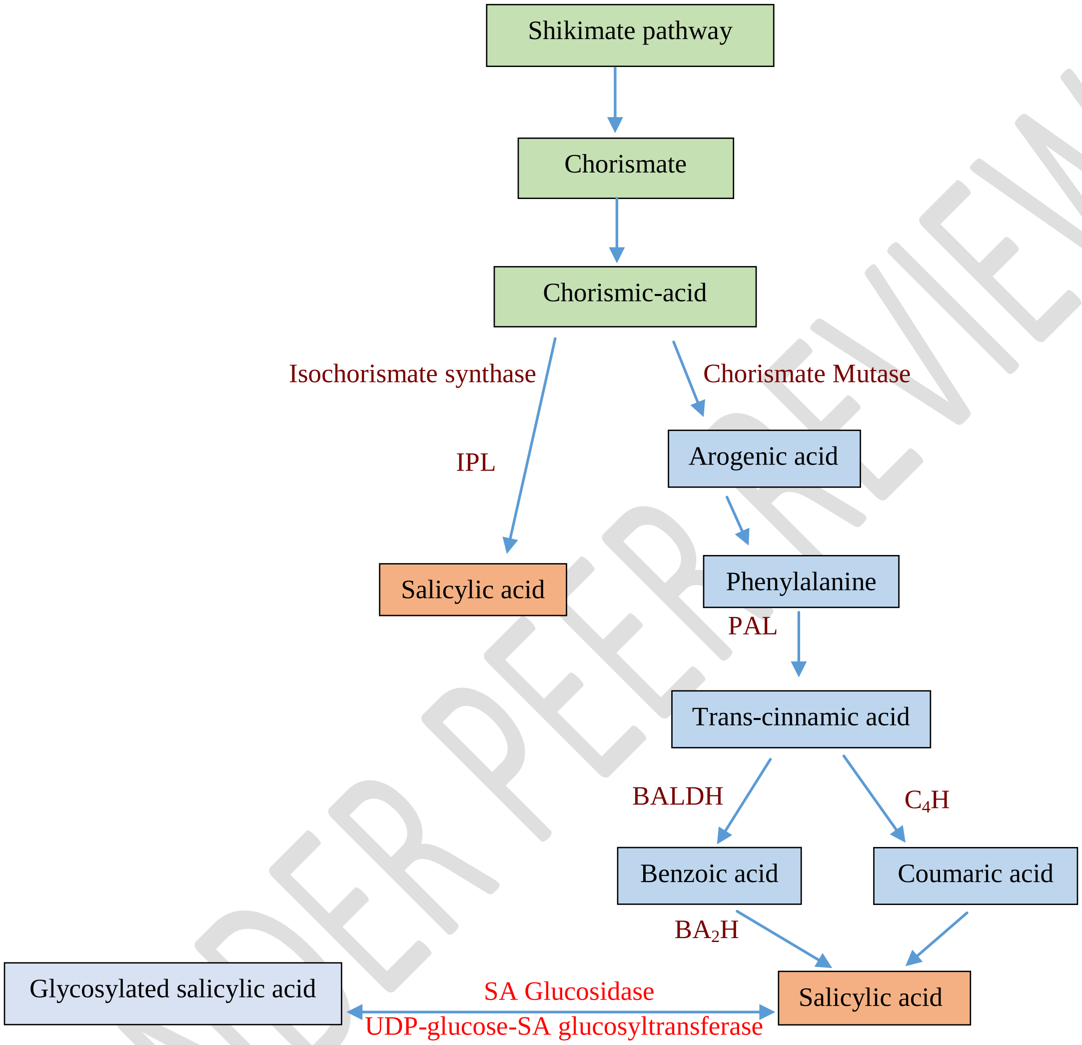

Fig. 1: Biosynthesis of salicylic acid (Source: Yang *et al*., 2023)

Signalling of Salicylic acid (SA)

Regulation of the SA biosynthesis pathway occurs at both the transcriptional and posttranscriptional stages. Plant transcriptional analysis has revealed the presence of MYBs (MY ELO BLAST; MYB 96 and MYB30), WRKYs (WRKY28 and WRKY46), and WIPK (Wound-Induced Transcription Factors of Mitogen-Activated Protein Kinase) genes. According to Vidhyasekaran (2015), these genes increase SA synthesis in plants by favorably regulating the isochorismate synthase pathway of the ICS gene encoding. An important part in establishing and signaling a defense response against diverse stressors is played by the well-known naturally occurring signaling molecule known as SA. For the downstream reaction to occur, the SA that plants make must be detected by its receptors. There are a number of SA-binding proteins (SABPs) that can detect SA. By influencing physiological and biochemical processes, salicylic acid functions as an endogenous natural signal molecule and is essential to defensive systems (Joseph *et al*., 2010). According to Kawano *et al*. (2004), salicylic acid produced by cells can readily enter and exit cells, tissues, and organs; and this movement is carefully controlled by ROS and Ca^{2+} (Chen *et al*., 2001). Additionally, SA was shown to engage in signalling and the control of gene expression during the senescence of Arabidopsis leaves Morris *et al*. (2000).

Salicylic acid functions as a signalling molecule and controls the formation of chloroplasts (Uzunova and Popova, 2000), photosynthetic activity (Fariduddin *et al*., 2003), gravitropism (Medvedev and Markova, 1991), and the prevention of fruit ripening (Srivastava and Dwivedi, 2000). Most genes and signaling pathways that are sensitive to salt and are in charge of cell death in response to salt stress are made more active by salicylic acid. These responsive genes produce the enzymes sinapyl alcohol dehydrogenase (SAD), cinnamyl alcohol dehydrogenase (CAD), and cytochrome P_{450}, which are all involved in secondary metabolite pathways. They also produce heat shock proteins (HSPs), chaperones, and chaperone-related proteins (Jumali *et al*., 2011). Ascorbate peroxidase (APX), glutathione reductase (GR), and superoxide dismutase (SOD) are part of the antioxidant system that SA activates to protect cells from stress (Gémes *et al*., 2011). By speeding up the rate of CO_2 absorption due to an increase in stomatal conductance, the exogenous application of SA (500 μM) relieved the drought stress in *Hordeum vulgare* (Habibi, 2012). The AsA-GSH pathway's enzymatic and nonenzymatic components are regulated by SA supplementation, which also helps plants subjected to drought to overcome oxidative stress (Alam *et al*., 2013). According to Miura *et al*. (2013), the expression of the *SIZ1* gene in *Arabidopsis thaliana* caused endogenous buildup of SA, which is crucial for stomatal closure under drought. Under low temperature stress, exogenous application of 0.5 mM SA also altered the activity of antioxidant enzymes such APX, SOD, GPOX, GSH-reductase, and GR and increased the chlorophyll fluorescence in Z. mays (Janda *et al*., 1999). In citrus fruits under cold stress, 2.0 mM SA was found to increase phenolic accumulation and PAL activity (Siboza *et al*., 2014). Under heat stress, Cucumis sativus produced more PSII, Fv/Fm, and quantum yields of the PSII electron transport when 1.0 mM SA was added (Shi *et al*., 2006). This was accomplished by reducing electrolyte leakage and oxidative stress. According to a study by Khan *et al*. (2013), the exogenous injection of 0.5 mM SA reduced the stress-induced synthesis of ethylene and hence the harmful consequences of heat stress.

“Salicylic acid is not the mobile signal itself, although SAR is still shown to occur in other parts of the plant. Furthermore, recent studies indicate that the volatile SAR signal produced by the methyl ester methyl salicylate is transmitted to remote parts of the plant, including neighboring plants” (Vlot *et al*., 2008). “Salicylic acid carboxyl methyltransferase (16 µM) converts salicylic acid (SA) to methyl salicylate (MeSA) in plants at low SA concentrations” (Dempsey *et al*., 2011). “Only the methylated form (MeSA) of SA has been demonstrated to travel regionally and systemically in plant tissue following pathogen infections” (Seskar *et al*., 1998). Therefore, MeSA was assumed to be the long-distance signaling molecule via phloem translocation, which travels from afflicted to unaffected leaves.

Salicylic acid (SA) roles in plant stress responses

The survival and development of plants are significantly impacted by a variety of stress elements in the plant growth environment, such as pathogen infection, dehydration, salt stress, etc. Plants have developed a number of stress-tolerance strategies involving the control of several cell signaling pathways (Khoshru *et al*., 2023). Salicylic acid (SA) is essential for plants to be able to withstand stress (Fig. 2).

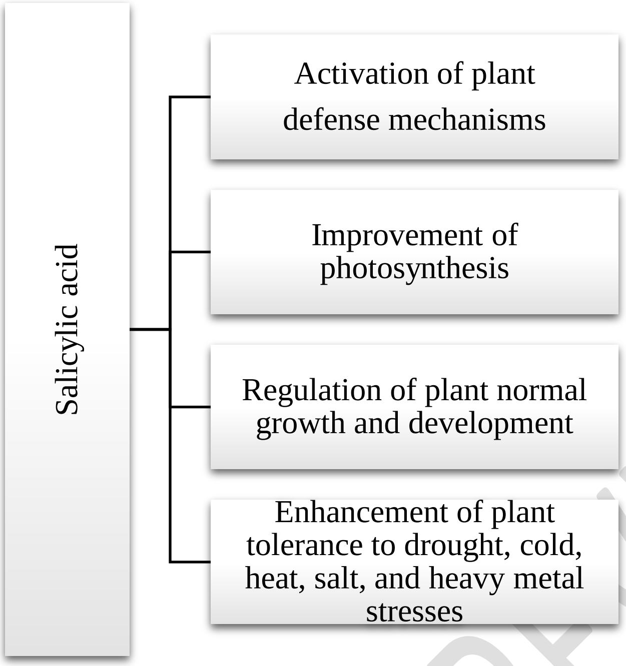

Fig. 2: SA main roles in plant tolerance to stresses (Source adapted from Khoshru *et al.*, 2023)

The direct involvement of SA in the activation of plant defense systems has been widely documented and examined (Table 1 & 2). SA may increase the activity and expression of antioxidant enzymes including superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) while it activates the appropriate plant defense mechanism (Alam *et al.*, 2022). A plant's resistance to biotic stressors brought on by pathogens, fungi, and pests can be increased while SA induces the production of active anti-pathogenic compounds (Ali *et al.*, 2018).

SA serves several functions in improving plant stress resistance, according to recent studies. The following categories may be used to group these roles of SA: immunological response (Cui *et al.*, 2018), antioxidative defense (Alam *et al.*, 2022), salt tolerance (Fu *et al.*, 2023), and drought tolerance (Chávez-Arias *et al.*, 2022). Numerous studies have shown that SA plays a key signaling role in plants' immunological responses to biotic and abiotic stress (Zhang *et al.*, 2022). In order to increase plant tolerance to diseases, it can control cell wall strengthening (Jia *et al.*, 2021), trigger the expression of a broad variety of disease resistance genes (Wang *et al.*, 2012), and promote hormone synthesis (Khan *et al.*, 2023). SA can also increase a plant's resilience to oxidative stress. For instance, studies have demonstrated that SA can increase the production of antioxidant enzymes, improving the plant's capacity to neutralize reactive oxygen species and lessen cellular oxidative damage (Hasanuzzaman *et al*., 2022). "SA is a crucial signaling molecule that activates responses to a variety of abiotic stressors, such as cold, heat, drought, salt, heavy metals, and others" (Widhalm and Dudareva, 2015). It also takes part in developmental signaling pathways necessary for optimal plant growth, such as blooming and senescence.

Table 1: Response of SA to plant biotic and abiotic stress

Stress Factors	**Plant Species**	**SA Roles**	**References**
Multiple pathogens	General plants	Activation of SAR pathways; defense response against biotrophic pathogens	Khoshru *et al*. 2023
Multiple biotic stresses	General plants	Activation of MAPK, CDPK, and other PKs; enhancement of SM biosynthesis	Anjali *et al*. 2023
Pathogens	*Arabidopsis*	Modulation of SA biosynthesis by SABC1's role as a molecular switch in balancing plant defense and growth	Liu *et al*. 2022
Bacterial pathogens	Jujube	Indication of antimicrobial activity	Aldhanhani *et al*. 2022
Insect herbivores and pathogens	General plants	Defense responses of SA induction to pathogens or aphid feeding	Musaqaf *et al*. 2023
Fungal pathogens	Apple	Significant upregulation of NPR1 and PR1; enhancement of endogenous SA; initiation of SA signaling pathway by (E)-2-Hexenal-based coating	Wang *et al*. 2022
Weeds	Crops	Alteration of crop growth by weeds through increment of SA signaling process	Horvath *et al*. 2023
Pests	Grapevines	Reduced injury by JA and SA application; reduction of number of eggs laid by D. suzukii females in JA- and SA-treated plants	Hussain *et al*. 2023

Abbreviations: SA (salicylic acid), SAR (systemic acquired resistance), SM (secondary metabolite), MAPK (mitogen-activated protein kinase), CDPK (calcium-dependent protein kinase), SABC1 (salicylic acid biogenesis controller 1), JA (jasmonic acid).

Table 2: Response of SA to plant abiotic stress

Stress Factors	**Plant Species**	**SA Roles**	**References**
Heat, cold	Citrus plants	Involvement in fruits' heat-induced cross-adaptation to chilling	Lafuente *et al*. 2022
Salt, drought	Rice	Regulation of stomatal aperture through the OsWRKY45-reactive oxygen pathway; regulation of adaptation to soil salinity and drought stress	Xu *et al*. 2023
Heavy metals	General plants	Induction of acclimatization impacts; improvement of tolerance against heavy metal stress	Rahman *et al*. 2023
	Common bean	Improvement of growth traits and photosynthetic indexes; enhancement of antioxidant enzyme activities and proline accumulation	Khalil *et al*. 2021
Heat	Maize	Significant elevation of transcripts of SA biosynthesis and signaling, and heat stress-responsive genes in SO_2 pretreated seedlings; improvement of seedlings' thermotolerance	Li *et al*. 2023
Drought	Wheat	Substantial reduction of drought influence, and enhancement of grain yield and water use efficiency by co application of K^+ and SA	Munsif *et al*. 2022
Dry climatic conditions	Wheat	Attenuation of deficit irrigation, and improvement of growth and production by co-application of essential plant nutrients and SA	Alotaibi *et al*. 2023
Cadmium	Tomato	Significant reduction of cell wall Cd accumulation; changes in Cd distribution	Jia *et al*. 2021
Waterlogging stress	Soybean	Reduction of some physiological indexes by SA and KN; enhancement of antioxidant defense by SA and KN; effective improvement of ROS metabolism and waterlogging stress tolerance	Hasanuzzaman *et al*. 2022
Water deficit and nutrient deprivation	*Sempervivum tectorum* L.	Strong positive correlation between SA and some physiological indexes; possible antagonistic modulation of ABA and SA on water deficit-induced morphological changes	Villadangos *et al*. 2023
Abiotic stresses	Horticultural crops	Provision of abiotic stress tolerance; elicitation of various physiological and morphological responses to stress;	Yang *et al*. 2023

		regulation of stress-responsive genes' expression; direct interaction with various hormones, proteins, and enzymes involved in abiotic stress tolerance	
Deficient irrigation	Potato	Significant enhancement of growth characteristics, yield components, and photosynthetic attributes	Desoky *et al*. 2021
Saline stress	General plants	Induction of saline stress tolerance	Yang *et al*. 2023

Abbreviations: SA (salicylic acid), ABA (abscisic acid), ROS (reactive oxygen species), Cd (cadmium), KN (kinetin).

Salicylic acid (SA) in plant growth and productivity

It has been demonstrated that SA has the ability to control the healthy growth and development of plants. Plants' physiological and biochemical processes are known to be affected by salicylic acid and other salicylates, which may be important in controlling plant growth and productivity. Salicylic acid plays a crucial role in plant physiological functions, such as increasing the plant's response to stress conditions (biotic and abiotic), increasing the plant's resistance to System Acquired Resistance (SAR), and stimulating or altering the internal endogenous signaling to withstand a variety of stresses. "Additionally, it has the capacity to form conjugates with certain amino acids, including proline and arginine, increasing the plant's ability to withstand environmental challenges and maintaining systemic acquired resistance. The generation of antioxidants is one of SA most significant impacts. The SA also plays a number of significant physiological activities, including promoting flowering, ion absorption, nutrition transfer, raising CO_2 representation, regulating stomatal movement, photosynthesis, gas exchange, and protein synthesis. In addition, it speeds up the production of different plant pigments and raises their levels, such as chlorophyll and carotene, and inhibits the representation of ethylene gas, which is in opposition to the function of ABA, which is responsible for the fall of leaves. Additionally, it plays a significant part in boosting metabolic rates, which helps the plant save energy by using alternate routes and changing its amount of nucleic and amino acids" (Davies, 2004).

When wheat seeds were treated with salicylic acid prior to planting, greater germination and seedling development were observed (Shakirova, 2007). According to Fariduddin *et al*. (2003), when lower amounts of salicylic acid were sprayed on Brassica juncea, the dry matter buildup was dramatically increased. Higher SA concentrations exhibited an inhibitory impact, though.

Laishram *et al*. 2020 reported significant growth and development of lentil under rainfed conditions owing to watersoluble antioxidant compound of SA which regulate the plant growth and development. The number of leaves and the fresh and dry mass per plant of wheat seedlings grown from grains soaked in a lower SA concentration (105 µM) both rose considerably (Hayat *et al*., 2005). Maize's carbohydrate content was improved by the exogenous SA treatment as well (Khodary, 2004). In their pot experiment, Hussein *et al*. (2007) sprayed salicylic acid on the leaves of wheat plants and watered them with water from the Mediterranean Sea. They found that this increased productivity resulted from improvements in all growth characteristics, including plant height, the number and area of green leaves, the diameter of the stem, and the dry weight of the stem, leaves, and plant as a whole. Additionally, the plants that were treated with SA had higher proline.

"Yield of lentil were increased significantly with seedpriming of SA @ 200ppm, as the growth promoting effect of SA which increased the level of cell division within the apical meristem of seedling root and caused higher plant growth and increased the dry matter production" (Laishram *et al*., 2023). SA can boost both the amount and quality of blooms. For instance, SA can affect blooming by encouraging flower buds to differentiate (Guo *et al*., 2023). In addition to modulating seedling growth, SA also affects seedling dormancy and development. There is evidence from several research that salicylic acid influences plant growth and productivity. Abbas and Ibrahim, 2014 reported that when SA was sprayed on Niggella sativa L. at different concentrations (50, 100, and 200 mg/l), it had a substantial impact on the examined attributes (growth, yield, and oil ratio). A study on *Datura stramonium* L. when sprayed with SA at 200ppm resulted that the maximum rate of all vegetative and investigated parameters (plant height, dry and vegetative content of the leaves, nitrogen and potassium, number of fruits, plant, and total yield kg/hectare) (Al-Mohammadi and Al-Rawi, 2016). According to Sandoval-Yapiz (2004), *Tagetus erecta* rooting was improved when salicylic acid levels were lower and a comparable promotion was also produced in the shoot system, increasing plant production. In rapeseed, the yield were enhanced significantly when the plants were sprayed with salicylic acid @ 200ppm (Wangkheirakpam *et al*., 2020). By comparing the combined effects of SA, GA, Kinetin, NAA, ethral, and chloro chloro chloride (CCC), Kumar *et al*. (2000) discovered that SA and GA had a synergistic impact on blooming when compared to other hormone combinations.

Salicylic acid may therefore be inferred to function as an endogenous regulator that may have an impact on plant development and production.

Conclusion

As a result of the foregoing explanation, it can be inferred that salicylic acid functions as a powerful plant growth regulator that is capable of modulating a variety of plant development responses. SA improves a plant's ability to grow and produce. Plants are significantly protected against a variety of biotic and abiotic stresses because to salicylic acid application's ability to trigger the SAR in plants. In addition to offering defense against pathogen and infection assaults, it also lessened the harmful effects caused by exposure to different abiotic stressors, such as heavy metals, temperature, water, and salinity stress, etc. Exogenous application of reduced salicylic acid concentrations improved plant growth during photosynthesis and a number of other physiological and biochemical traits. However, SA itself has the potential to put plants under a lot of stress at greater concentrations. Additionally, SA boosts the functions of the antioxidant enzyme system and can safeguard and improve the nitrate metabolism enzymes in high-stress environments.

Future perspectives

Salicylic acid functions physiologically in a variety of ways in plants and may be able to lessen the harmful impacts of numerous biotic and abiotic stressors. However, more work still has to be done to clarify the precise routes of its biosynthesis, whether significant or minor, as well as its mode of action and other unique and cooperative regulatory roles played by SA that have up to now eluded researchers. The study of how this plant hormone interacts and is controlled by cross-talk in harmony with other recognized phytohormones and plant growth regulators working at long range (auxins, cytokinins, gibberellins, ethylene, etc.), short range (NO, jasmonates, brassinosteroids, etc.), and very short range (ROS, H_2O_2) is also necessary. Another argument may be made that these short-range phytohormones are mostly synthesized nearby biotic infestations and then transferred systemically to function during widespread abiotic pressures. Clarifying the function of the aforementioned phytohormone in the tissue-specific differentiation and growth of plant parts throughout growth and development is also important. Mutant research and biochemical inhibitors of important enzymes and pathways may provide some light on these issues. This problem could be resolved by identifying tissue-specific concentrations when seedlings are developing and fusing them with reporter genes or radioactive compounds. Exogenous application of this phytohormone may prove to be an effective strategy in the future for promoting plant growth and production as well as thwarting the negative effects brought on by various abiotic stressors. Future uses of this plant hormone as a management tool to help our agricultural crops adapt to the aforementioned constraints offer enormous promise for accelerating crop output potential in the near future.

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