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Current Knowledge on the Role of Salicylic Acid for Stress Tolerance on Field Crops

Aritra Guin [a*], Santosh Korav [a], Biswajyoti Banik [a] and Denil Unjia [a]

[a] *Department of Agronomy, School of Agriculture, Lovely Professional University, Phagwara, Jalandhar, Punjab, 144411, India.*

Authors' contributions

This work was carried out in collaboration among all authors. Authors AG and SK framed the article. Authors AG, BB and DU composed the research findings and wrote the article. Author SK edited and proofread the manuscript. All authors read and approved the final manuscript.

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Review Article

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ABSTRACT

Salicylic acid is a well-known signal molecule that mediates plant resistance and is also involved in the control of plant development. Conversely, despite its well-established role in plant resistance, its impact on plant development is still poorly understood. the body of research indicating the essential functions of salicylic acid in controlling cell division and expansion, two processes that ultimately determine a plant's structure. This study summarizes the current knowledge of the mechanisms and molecular mechanisms via which salicylic acid regulates plant development through a range of pathways. Here, the role of salicylic acid in controlling growth regulation through effects on cell division and expansion is highlighted. The methods and molecular processes by which salicylic acid controls stress tolerance through a variety of pathways are compiled in this study. The relationships between salicylic acid and other hormones

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**Corresponding author: E-mail: aritraguin2@gmail.com;*

as well as their significance in determining plant development were also covered. Future crop improvement will greatly benefit from a deeper understanding of the process underpinning salicylic acid-mediated growth.

Keywords: Cell division; hormones; plant resistance; salicylic acid.

1. INTRODUCTION

Ortho-hydroxybenzoic acid, or salicylic acid (SA) — derived from the Latin word *Salix*, which means willow tree — is another name for the phenolic derivative that is widely found in the plant kingdom and is recognized for its ability to regulate several physiological and biochemical processes, including plant signaling or defense mechanism, thermogenesis, and response to different abiotic and biotic stress [1,2]. Salicylic acid may be extracted from plants in both free and conjugated form, and it is a member of a broad class of plant phenolics from a chemical perspective. The conjugated form is the aromatic ring being hydroxylated, methylated, and/or glucosylated [3,4]. Johan Büchner first extracted salicin, one of the naturally occurring salicylic acid derivatives, from the willow tree's (*Salix* sp.) bark in 1828 [5,6]. The concentration of this natural compound in plants varies significantly with the seasons by 3 mg/g of fresh biomass in *S. laponum* plants [7]. The highest content of salicylic acid is found in spring and summer and the lowest content in autumn and winter. Subsequently, it was found that nearly all willow trees, including *Salix daphnoides*, *Salix purpurea*, *Salix alba*, and *Salix fragilis* were particularly rich in it [7]. The Italian chemist Raffaele Piria obtained salicylic acid in the bloom and buds of the European plant *Spiraea ulmaria*, later renamed *Filipendula ulmaria* (L.) Maxim. Piria was the first scientist to find this natural substance in species other than *Salix* sp. in late 1838. The identification of these phytohormones as non-specific to the *Salix* genus has allowed for further research into its production, biochemical properties, and physiological roles in plants [8].

In terms of production, two metabolic pathways are known to produce salicylic acid via the shikimate pathway in terms of its production. The first route—also referred to as the phenylalanine route—occurs in the cytoplasm of the cell. Trans-cinnamic acid (t-CA), which is oxidized to benzoic acid (BA) is produced by the enzyme phenylalanine ammonia lyase (PAL) from phenylalanine (Phe). Salicylic acid is subsequently formed via the hydroxylation of the aromatic ring of benzoic acid (BA), which is catalyzed by the enzyme benzoic-acid-2-hydroxylase (BA2H). Hydrogen peroxide (H_2O_2) must be present for BA2H to convert benzoic acid (BA) into salicylic acid [9- 11]. The initial evidence for the first pathway came from Ellis and Amrchein, who noted that salicylic acid was produced when *Gaultheria procumbens* plants were fed with 14C-cinnamic acid or 14C-benzoic acid [12]. Nevertheless, new findings suggest that salicylic acid is most likely derived directly from benzoyl glucose, a conjugated form of benzoic acid (BA) [11,13]. The second step, known as the isochorismate (IC) pathway, takes place within the chloroplast [14- 16]. Isochorismate pyruvate lyase (IPL) and Isochorismate synthase (ICS) are the two enzymes that catalyze the conversion of chorismate in plants into isochorismate and ultimately salicylic acid.

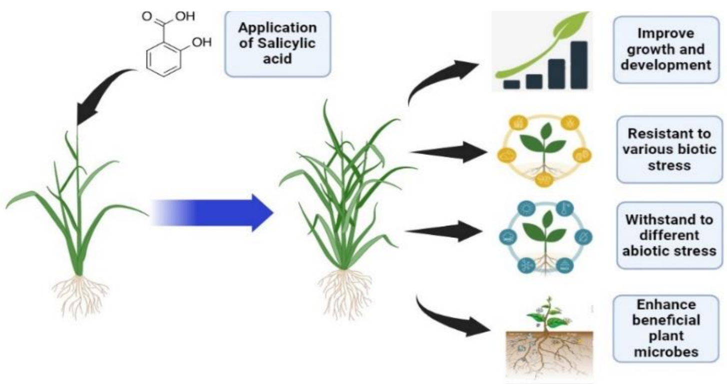

Fig. 1. Various effects of salicylic acid on field crops

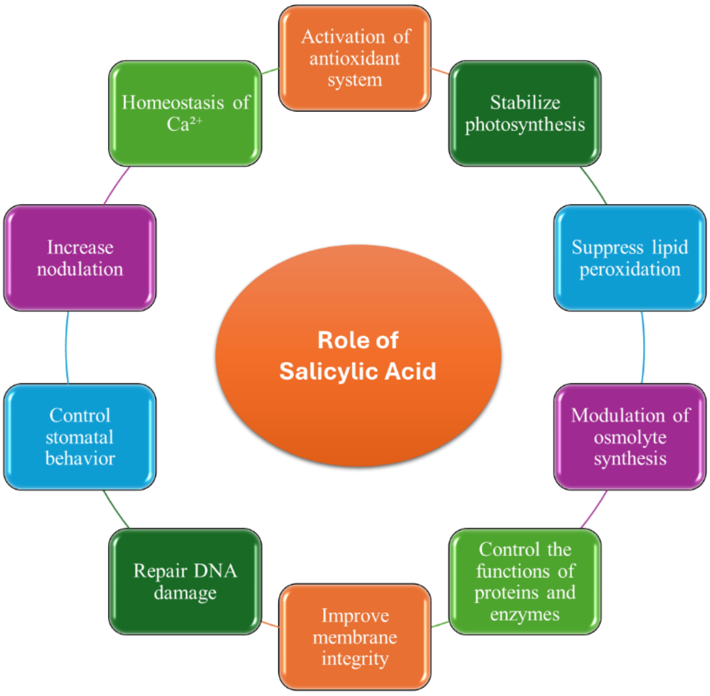

Fig. 2. Role of Salicylic acid on growth and development of field crops

It is well recognized from a physiological perspective that salicylic acid is essential for controlling plant development and growth regulation, defense against different abiotic and biotic stress, and immunological responses (Fig 1) [4,17- 21]. From that point on, there was an exponential rise in the number of articles focusing on salicylic acid as a plant growth regulator, signaling molecule, and plant elicitor that protects plants from different abiotic and biotic stresses [20- 27]. The current study provides an extensive compilation of data on the roles that salicylic acid plays in plant stress tolerance as well as plant growth and development by focusing on these factors (Fig 2). The goal is to provide a clear image of salicylic acid and aid in directing further studies on this subject.

2. LITERATURE REVIEW

2.1 The Role of Salicylic Acid on Growth and Development of Plants

Salicylic acid may exhibit controversial roles in the growth and development of plants, contingent on its concentration, the plant's growing environment, and its stage of development [28]. Elevated levels of salicylic acid can often impede the growth and development of plants (which is contingent upon the plant type; however, concentrations exceeding 1 mM are deemed high). Nevertheless, utilizing appropriate doses of salicylic acid has advantageous effects. Salicylic acid has been shown to promote growth in various plant species under both normal and diverse abiotic stress conditions [29].

Exogenous salicylic acid application diversely impacts plant growth, such as seed germination, budding, blooming, fruit setting, and ripening. Salicylic acid-induced blooming in finger millet plants [30]. Seed germination of maize and barley was inhibited when infused with more than 3 mM of salicylic acid [31]. However, ingesting maize seeds by 0.3 mM - 0.9 mM salicylic acid resulted in increased shoot length, germination rate, and germination percentage [32]. The strongest germination-stimulating impact was notably shown by 0.43 mM salicylic acid; however, at higher doses, its effect was diminished. So, various salicylic acid can either promote or inhibit plant growth in various plant species.

2.2 The Role of Salicylic Acid on Biotic Stress Tolerance

Salicylic acid is a plant defense-related hormone essential for resistance to several microbial diseases, including fungi, bacteria, viruses, and oomycetes [33]. It is widely known that endogenous salicylic acid levels in plants are positively correlated with resistance mechanisms to both biotrophic and hemibiotrophic diseases [34]. Additionally, the use of exogenous salicylic acid induces local and systemic acquired resistance to several pathogens, such as *Alternaria alternata*, *Fusarium oxysporum*, *Colletotrichum gloeosporides*, *Magnaporthe grisea*, *Xanthomonas* spp., various viruses, and so forth [35- 37] (Table 1). Notably, the growth of the powdery mildew disease in cucumber plants was almost entirely inhibited by the exogenous application of salicylic acid. Due to its intricacy, salicylic acid's functions in plant defense against necrotrophic diseases are yet unclear. There have been a few reports of exogenous salicylic acid treatment-induced higher sensitivity among various plant-necrotrophic pathogen interactions. Salicylic acid treatment in broad beans reduced red light-induced resistance to the necrotrophic fungus *Botrytis cinerea*, but it did not increase black light-induced vulnerability [38]. Application of tomato SA-induced increased susceptibility in a dose-established way against *B. cinerea*. It is also controversially suggested that salicylic acid increases the resistance of Arabidopsis and tomato plants to *B. cinerea* [39,40].

2.3 The Role of Salicylic Acid on Abiotic Stress Tolerance

Plant productivity is threatened by climate change and continuous crop production due to several abiotic stressors, including salinity, ozone, UV light, temperature, drought, and heavy metals [46]. It is interesting to note that in addition to resistance to biotic stresses, salicylic acid regulates tolerance to various abiotic stimuli [47] (Table 2). The following are the mechanisms of salicylic acid-induced abiotic stress tolerance: (1) accumulation of osmolytes that can support the maintenance of osmotic homeostasis; (2) regulating minerals absorption; (3) increased activity of scavenging reactive oxygen species; (4) increased production of secondary metabolites, including nitrogen (alkaloids, non-protein amino acids, and cyanogenic glucosides,) and sulphur-containing compounds (allinin, glutathione, thionins, phytoalexins, defensins, and glucosinolates) and (5) control of additional hormone pathways [47,48].

A group of pathogenesis-related (*PR*) genes, including *PR1*, *PR2*, and *PR5*, are expressed upon exogenous salicylic acid treatment is applied [49]. Transgenic overexpression of several *PR* genes improved tolerance to various abiotic stressors as well as resistance to various infections [50- 52]. Increased resistance to heavy metals was shown by transgenic tobacco that overexpressed pepper *PR-1* [51]. In *Arabidopsis* plants, overexpression of pepper *PR-1* increased resistance to salt and drought stress [50]. Additional studies are needed to understand the underlying molecular processes by which these PR proteins enhance resistance to abiotic stress.

Table 1. Enhancement of disease resistance mechanism by foliar spray of SA in different plants

Host	Pathogen	Salicylic acid concentration	Effect	Reference
Oryza sativa (Rice)	*Xanthomonas oryzae*	1 mM	Reduction of leaf blight lesion	[41]
		1 mM	Reduction of severity of disease (30%)	[42]
	Magnaporthe grisea	8 mM	Reduction of severity of disease (70%)	[43]
	Oebalus pugnax	16 mM	Reduce the number of bugs (35%)	[44]
Cicer arietinum (Chickpea)	*Fusarium oxysporum*	14.5 mM (stem)	Reduction of severity of disease (20%)	[45]
		0.58 mM (soil)	Reduction of severity of disease (20 %)	
Vigna mungo (Black gram)	*Mungbean yellow mosaic Indian virus (MYMIV)*	0.1 mM	Reduction of severity of disease (71%)	[36]

2.4 Salicylic Acid and Plant Microbes

The plant science community has recently shown increased interest in studies examining the relationship between plant health and the microbiome [57, 58]. The impact of salicylic acid on the microbiome of the model plant Arabidopsis thaliana was examined using either exogenous salicylic acid application or mutants with changed endogenous salicylic acid levels [59]. Results showed that the application of salicylic acid significantly increased the amount of certain bacterial isolates from the Synthetic Community (SynCom) experiment and decreased the amount of *Mitsuaria* sp. 370 (β-Proteobacteria). Furthermore, in *cpr5* mutants that constitutively manufacture salicylic acid, the population densities of 12 groups of Proteobacteria and nine Actinobacteria groups was decreased and raised, respectively. This implies that salicylic acid may significantly change the microbiome of the soil or rhizosphere. Stimulation of the systemic immune response has so far been the main effect of salicylic acid effects on plants so far after soil drench application; however, not much is known about the effects of compounds on endophytic microbiomes or plant roots [60].

2.5 Salicylic Acid with Other Plant Growth Regulators (PGRs)

Salicylic acid controls many plant responses by interacting with other plant growth regulators or plant hormones under both favorable and unfavorable conditions. Under both ideal and stressful conditions, the relationship between salicylic acid and other hormones, including cytokinin, auxin, gibberellins, abscisic acid, brassinosteroids, and ethylene has been investigated. In stressful situations, the interaction between salicylic acid and hormones may have an antagonistic or synergistic effect. Tamás et al. [61] recently examined how salicylic acid controlled the reduction of Cd-induced auxin-mediated ROS (reactive oxygen species) generation in barley roots, hence mitigating Cd stress. The authors hypothesize that salicylic acid plays a part in the IAA (indole-3-acetic acid) signaling system since salicylic acid treatment reduces the stress responses that IAA generates in plants. Agtuca et al. [62] documented that salicylic acid and IAA had opposing roles in maize roots. IAA applied exogenously promoted lateral development by inhibiting primary root growth, while salicylic acid increased the total root biomass [62].

Table 2. Exogenous application of SA in various plants increases their resistance to abiotic stresses

Host	Abiotic stress	Salicylic acid concentration	Effect	Reference
Triticum aestivum (Wheat)	Freezing	0.01, 0.1, and 1 mM	Cell mortality and the loss of PS II quantum yield brought on by freezing stress were dramatically reduced by 0.01 mM and 0.1 mM salicylic acid.	[53]
Zea mays (Maize)	Cadmium (Cd)	0.5 mM	Root DW and shoot FW are raised by around 121% and 262%, respectively.	[54]
Hordeum vulgare (Barley)	Cadmium (Cd)	0.5 mM	Root DW and shoot FW are raised by around 127% and 133%, respectively.	[55]
	Osmotic stress	30, 60, and 120 nM	Approximately 50% less osmotic stress-induced membrane damage occurred.	[56]

Plants may experience oxidative stress and increased ethylene production when exposed to several environmental conditions, such as heavy metals (HM) [47]. Peak expression of ethylene-related biosynthetic genes or expression of ethylene-responsive genes is the cause of the enhanced ethylene synthesis. The exogenous spray of salicylic acid helped wheat under Cd stress by raising GSH levels, which led to metal detoxification and scavenged ROS (reactive oxygen species) produced by HM (heavy metals)-triggered ethylene synthesis. Addition of salicylic acid under Cd stress increased abscisic acid (ABA) levels in wheat seedlings, which were linked to the biosynthesis of ABA [63]. Additionally, during HM stress, endogenous ABA regulated SA-mediated changes in dehydrin protein concentration, indicating the protective function of salicylic acid in wheat plants [63].

Crosstalk between salicylic acid and jasmonate is required to regulate plant development in the presence of abiotic stressors [64, 65]. The signaling pathways for jasmonic acid and salicylic acid often function antagonistically. The antagonistic effect between salicylic acid and jasmonic acid cell signaling is mediated by the Mitogen-Activated Protein Kinase (MAPK) signaling pathway [66]. Nonantagonistic interactions between salicylic acid and jasmonic acid have also been recorded, although further research is necessary to determine the precise mechanism [64]. Cu stress caused salicylic acid production in maize plants, which in turn caused jasmonic acid priming and jasmonic acid-induced volatile organic molecules.

3. CONCLUSION

Salicylic acid and its derivatives are promising as environmentally friendly plant protection products because of their positive effects on plant and human health. Determining the optimal concentration from micromolar to low millimolar levels is important to provide disease resistance without interfering with plant growth. Higher concentrations of 2 mM can act as effective growth regulators to slow development and control disease. Research into natural salicylic acid derivatives, such as amorphutin, with improved efficacy may lead to the development of more effective plant protection methods. Further research is needed to understand the practical applications of salicylic acid in various crop species and to develop sustainable and cost-effective crop management systems using these versatile compounds.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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