

# **Current Knowledge on the Role of Salicylic Acid for Stress Tolerance on field Crops**

## **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 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. lapponum* 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

35 identification of these phytohormones as non-specific to the *Salix* genus has allowed for further  
36 research into its production, biochemical properties, and physiological roles in plants [8].

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

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

59

60

61

62

63

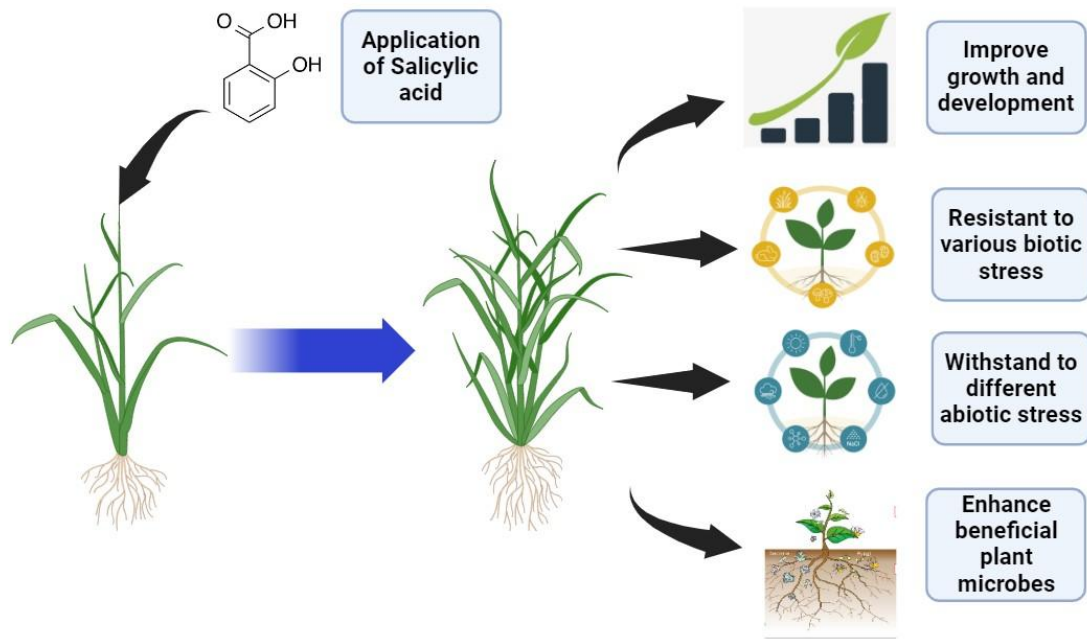
64

65

66

67

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



68

## 69 2. LITERATURE REVIEW

### 70 2.1 The role of salicylic acid on growth and development of plants

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

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

85

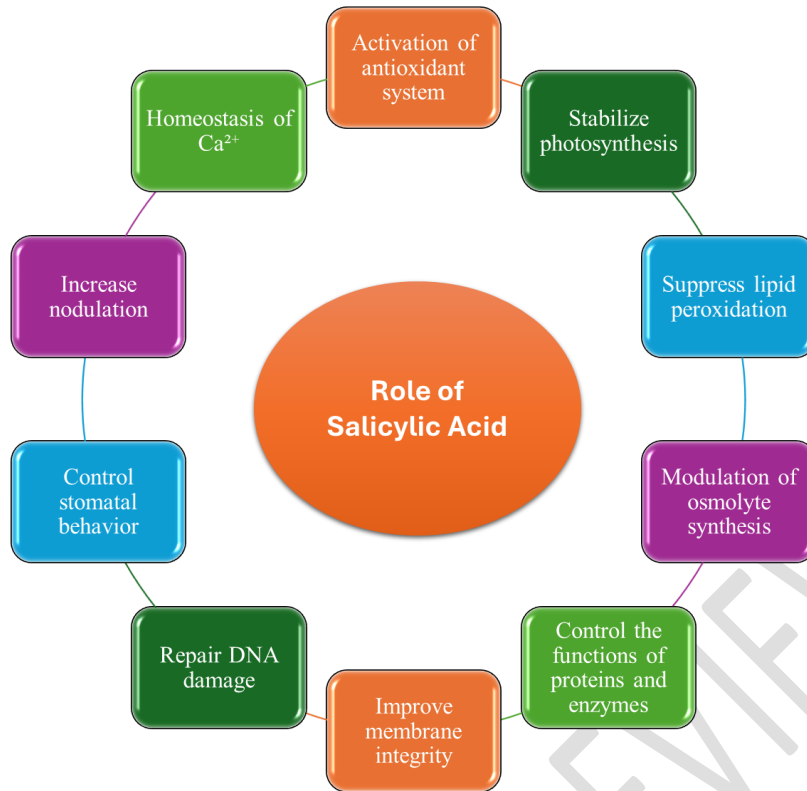
86

87

88

89

90  
91  
92  
93  
94  
95  
96  
97  
98  
99  
100  
101  
102  
103  
104  
105  
106  
107  
108  
109  
110  
111  
112  
113  
114  
115  
116  
117  
118



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

**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 gloeosporoides*, *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].

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

Host	Pathogen	Salicylic acid concentration	Effect	Reference
<i>Oryza sativa</i> (Rice)	<i>Xanthomonas oryzae</i>	1 mM	Reduction of leaf blight lesion	[41]
		1 mM	Reduction of severity of disease (30%)	[42]

	<i>Magnaporthe grisea</i>	8 mM	Reduction of severity of disease (70%)	[43]
	<i>Ooebalus pugnax</i>	16 mM	Reduce the number of bugs (35%)	[44]
<i>Cicer arietinum</i> (Chickpea)	<i>Fusarium oxysporum</i>	14.5 mM (stem)	Reduction of severity of disease (20%)	[45]
		0.58 mM (soil)	Reduction of severity of disease (20 %)	
<i>Vigna mungo</i> (Black gram)	<i>Mungbean yellow mosaicIndian virus (MYMIV)</i>	0.1 mM	Reduction of severity of disease (71%)	[36]

119

### 120 2.3 The role of salicylic acid on abiotic stress tolerance

121 Plant productivity is threatened by climate change and continuous crop production due to several  
 122 abiotic stressors, including salinity, ozone, UV light, temperature, drought, and heavy metals [46]. It is  
 123 interesting to note that in addition to resistance to biotic stresses, salicylic acid regulates tolerance to  
 124 various abiotic stimuli[47] (Table 2). The following are the mechanisms of salicylic acid-induced abiotic  
 125 stress tolerance: (1) accumulation of osmolytes that can support the maintenance of osmotic  
 126 homeostasis; (2) regulating minerals absorption; (3) increased activity of scavenging reactive oxygen  
 127 species; (4) increased production of secondary metabolites, including nitrogen (alkaloids, non-protein  
 128 amino acids, and cyanogenic glucosides,) and sulphur-containing compounds (allinin, glutathione,  
 129 thionins, phytoalexins, defensins, and glucosinolates) and (5) control of additional hormone pathways  
 130 [47,48].

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

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

Host	Abiotic stress	Salicylic acid concentration	Effect	Reference
<i>Triticum aestivum</i> (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]
<i>Zea mays</i> (Maize)	Cadmium (Cd)	0.5 mM	Root DW and shoot FW are raised by around 121% and 262%, respectively.	[54]
<i>Hordeum vulgare</i>	Cadmium (Cd)	0.5 mM	Root DW and shoot FW	[55]

(Barley)

Osmotic stress

30, 60, and 120  
nM

are raised by around  
127% and 133%,  
respectively.  
Approximately 50% less  
osmotic stress-induced  
membrane damage  
occurred.

[56]

140

#### 141 **2.4 Salicylic acid and plant microbes**

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

#### 154 **2.5 Salicylic acid with other plant growth regulators (PGRs)**

155 Salicylic acid controls many plant responses **by interacting** with other plant growth regulators or plant  
156 hormones **under both favorable and unfavorable conditions**. Under both ideal and stressful conditions,  
157 the relationship between salicylic acid and other hormones, including cytokinin, auxin, gibberellins,  
158 abscisic acid, brassinosteroids, and ethylene has been investigated. In stressful situations, the  
159 interaction between salicylic acid and hormones may have an antagonistic or synergistic effect.  
160 Tamás et al. (2015) [61] recently examined how salicylic acid controlled the reduction of Cd-induced  
161 auxin-mediated ROS (reactive oxygen species) generation in barley roots, hence mitigating Cd stress.  
162 The authors hypothesize that salicylic acid plays a part in the IAA (indole-3-acetic acid) signaling  
163 system since salicylic acid treatment reduces the stress responses that IAA generates in plants.  
164 Agtuca et al. (2014) [62] documented that salicylic acid and IAA had opposing roles in maize roots. IAA  
165 applied exogenously promoted lateral development by inhibiting primary root growth, while salicylic  
166 acid increased the total **root biomass** [62].

167 Plants may experience oxidative stress and increased ethylene production when exposed to several  
168 environmental conditions, such as heavy metals (HM) [47]. **Peak** expression of ethylene-related  
169 biosynthetic genes or expression of ethylene-responsive genes is the cause of the enhanced ethylene  
170 synthesis. The exogenous spray of salicylic acid helped wheat under Cd stress by raising GSH levels,  
171 which led to metal detoxification and scavenged ROS (reactive oxygen species) produced by  
172 HM (heavy **metals**)-triggered ethylene synthesis. **Addition of salicylic acid under Cd stress increased**

173 abscisic acid (ABA) levels in wheat seedlings, which were linked to the biosynthesis of ABA [63].  
174 Additionally, during HM stress, endogenous ABA regulated SA-mediated changes in dehydrin protein  
175 concentration, indicating the protective function of salicylic acid in wheat plants [63].

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

### 184 3. CONCLUSION

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

### 194 ACKNOWLEDGEMENTS

195 The authors would like to acknowledge the School of Agriculture, Lovely Professional University for  
196 their consistent support in writing this review paper.

### 197 COMPETING INTEREST

198 The authors have declared that no competing interests exist.

### 199 AUTHOR'S CONTRIBUTION

200 Aritra Guin and Santosh Korav have selected the review article's topic and framed the review article.  
201 Aritra Guin, Biswajyoti Banik, and Denil Unjiacomposed all the research findings and wrote the review  
202 article. The final editing and proofreading were done by Santosh Korav.

### 203 REFERENCES

204 1. Chen Z, Zheng Z, Huang J, Lai Z, Fan B. Biosynthesis of salicylic acid in plants. Plant signaling &  
205 behavior. 2009;4(6):493-496. DOI: <https://dx.doi.org/10.4161/psb.4.6.8392>

- 206 2. Wani AB, Chadar H, Wani AH, Singh S, Upadhyay N. Salicylic acid to decrease plant stress.  
207 Environmental Chemistry Letters. 2017;15(1):101-123. DOI: [https://dx.doi.org/10.1007/s10311-](https://dx.doi.org/10.1007/s10311-016-0584-0)  
208 016-0584-0
- 209 3. Lovelock DA, Šola I, Marschollek S, Donald CE, Rusak G, van Pée KH, Ludwig-Müller J, Cahill  
210 DM. Analysis of salicylic acid-dependent pathways in *Arabidopsis thaliana* following infection with  
211 *Plasmodiophorab Brassicae* and the influence of salicylic acid on disease. Molecular plant  
212 pathology. 2016;17(8):1237-1251. DOI: <https://dx.doi.org/10.1111/mpp.12361>
- 213 4. Maruri-López I, Aviles-Baltazar NY, Buchala A, Serrano M. Intra and extracellular journey of the  
214 phytohormone salicylic acid. Frontiers in Plant Science. 2019;10:455069. DOI:  
215 <https://dx.doi.org/10.3389/fpls.2019.00423>
- 216 5. Raskin I. Role of salicylic acid in plants. Annual review of plant biology. 1992;43(1):439-463.
- 217 6. Muthulakshmi S, Lingakumar K. Role of salicylic acid (SA) in plants—A review. Int. J. Appl. Res.  
218 2017;3(3):33-37.
- 219 7. Petrek J, Havel L, Petrlova J, Adam V, Potesil D, Babula P, Kizek R. Analysis of salicylic acid in  
220 willow barks and branches by an electrochemical method. Russian Journal of Plant Physiology.  
221 2007;54:553-558. DOI: <https://dx.doi.org/10.1134/S1021443707040188>
- 222 8. Sharma A, Sidhu GP, Araniti F, Bali AS, Shahzad B, Tripathi DK, Brestic M, Skalicky M, Landi M.  
223 The role of salicylic acid in plants exposed to heavy metals. Molecules. 2020;25(3):540. DOI:  
224 <https://dx.doi.org/10.3390/molecules25030540>
- 225 9. Shine MB, Yang JW, El-Habbak M, Nagyabhyru P, Fu DQ, Navarre D, Ghabrial S, Kachroo P,  
226 Kachroo A. Cooperative functioning between phenylalanine ammonia lyase and isochorismate  
227 synthase activities contributes to salicylic acid biosynthesis in soybean. New Phytologist.  
228 2016;212(3):627-636. DOI: <https://dx.doi.org/10.1111/nph.14078>
- 229 10. Zhang Y, Fu X, Hao X, Zhang L, Wang L, Qian H, Zhao J. Molecular cloning and promoter  
230 analysis of the specific salicylic acid biosynthetic pathway gene phenylalanine ammonia-lyase  
231 (AaPAL1) from *Artemisia annua*. Biotechnology and Applied Biochemistry. 2016;63(4):514-524.  
232 DOI: <https://dx.doi.org/10.1002/bab.1403>
- 233 11. Chong J, Pierrel MA, Atanassova R, Werck-Reichhart D, Fritig B, Saindrenan P. Free and  
234 conjugated benzoic acid in tobacco plants and cell cultures. Induced accumulation upon elicitation  
235 of defense responses and role as salicylic acid precursors. Plant Physiology. 2001;125(1):318-28.  
236 DOI: <https://dx.doi.org/10.1104/pp.125.1.318>
- 237 12. Hayat S, Ali B, Ahmad A. Salicylic acid: biosynthesis, metabolism and physiological role in plants.  
238 Salicylic acid: A plant hormone. 2007:1-4.
- 239 13. Yalpani N, León J, Lawton MA, Raskin I. Pathway of salicylic acid biosynthesis in healthy and  
240 virus-inoculated tobacco. Plant physiology. 1993;103(2):315-321. DOI:  
241 <https://dx.doi.org/10.1104/pp.103.2.315>
- 242 14. Métraux JP. Recent breakthroughs in the study of salicylic acid biosynthesis. Trends in plant  
243 science. 2002;7(8):332-334. DOI: [https://dx.doi.org/10.1016/S1360-1385\(02\)02313-0](https://dx.doi.org/10.1016/S1360-1385(02)02313-0)
- 244 15. Garcion C, Lohmann A, Lamodièrre E, Catinot J, Buchala A, Doermann P, Métraux JP.  
245 Characterization and biological function of the *ISOCHORISMATE SYNTHASE2* gene of

- 246 Arabidopsis. Plant physiology. 2008;147(3):1279-1287. DOI:  
247 <https://dx.doi.org/10.1104/pp.108.119420>
- 248 16. Rekhter D, Lüdke D, Ding Y, Feussner K, Zienkiewicz K, Lipka V, Wiermer M, Zhang Y, Feussner  
249 I. Isochorismate-derived biosynthesis of the plant stress hormone salicylic acid. Science.  
250 2019;365(6452):498-502. DOI: <https://dx.doi.org/10.1126/science.aaw1720>
- 251 17. Wei Y, Liu G, Chang Y, He C, Shi H. Heat shock transcription factor 3 regulates plant immune  
252 response through modulation of salicylic acid accumulation and signalling in cassava. Molecular  
253 plant pathology. 2018;19(10):2209-2220. DOI: <https://dx.doi.org/10.1111/mp.12691>
- 254 18. Hartmann M, Zeier J. N-hydroxypipelicolic acid and salicylic acid: a metabolic duo for systemic  
255 acquired resistance. Current opinion in plant biology. 2019;50:44-57. DOI:  
256 <https://dx.doi.org/10.1016/j.cpb.2019.02.006>
- 257 19. El-Shazoly RM, Metwally AA, Hamada AM. Salicylic acid or thiamin increases tolerance to boron  
258 toxicity stress in wheat. Journal of plant Nutrition. 2019;42(7):702-722. DOI:  
259 <https://dx.doi.org/10.1080/01904167.2018.1549670>
- 260 20. Luo J, Xia W, Cao P, Xiao ZA, Zhang Y, Liu M, Zhan C, Wang N. Integrated transcriptome  
261 analysis reveals plant hormones jasmonic acid and salicylic acid coordinate growth and defense  
262 responses upon fungal infection in poplar. Biomolecules. 2019;9(1):12. DOI:  
263 <https://dx.doi.org/10.3390/biom9010012>
- 264 21. Pasternak T, Groot EP, Kazantsev FV, Teale W, Omelyanchuk N, Kovrizhnykh V, Palme K,  
265 Mironova VV. Salicylic acid affects root meristem patterning via auxin distribution in a  
266 concentration-dependent manner. Plant Physiology. 2019;180(3):1725-1739. DOI:  
267 <https://dx.doi.org/10.1104/pp.19.00130>
- 268 22. Dempsey DM, Klessig DF. How does the multifaceted plant hormone salicylic acid combat  
269 disease in plants and are similar mechanisms utilized in humans?. BMC biology. 2017;15:1-11.  
270 DOI: <https://dx.doi.org/10.1186/s12915-017-0364-8>
- 271 23. Klessig DF, Choi HW, Dempsey DM. Systemic acquired resistance and salicylic acid: past,  
272 present, and future. Molecular plant-microbe interactions. 2018;31(9):871-888. DOI:  
273 <https://dx.doi.org/10.1094/MPMI-03-18-0067-CR>
- 274 24. Subban K, Subramani R, Srinivasan VP, Johnpaul M, Chelliah J. Salicylic acid as an effective  
275 elicitor for improved taxol production in endophytic fungus *Pestalotiopsis microspora*. PloS one.  
276 2019;14(2):e0212736. DOI: <https://dx.doi.org/10.1371/journal.pone.0212736>
- 277 25. Tripathi D, Raikhy G, Kumar D. Chemical elicitors of systemic acquired resistance—Salicylic acid  
278 and its functional analogs. Current Plant Biology. 2019;17:48-59. DOI:  
279 <https://dx.doi.org/10.1016/j.cpb.2019.03.002>
- 280 26. Nadeem M, Ahmad W, Zahir A, Hano C, Abbasi BH. Salicylic acid-enhanced biosynthesis of  
281 pharmacologically important lignans and neo lignans in cell suspension culture of *Linum*  
282 *ussitatisimum* L. Engineering in Life Sciences. 2019;19(3):168-74. DOI:  
283 <https://dx.doi.org/10.1002/elsc.201800095>

- 284 27. Li N, Han X, Feng D, Yuan D, Huang LJ. Signaling crosstalk between salicylic acid and  
285 ethylene/jasmonate in plant defense: do we understand what they are whispering?. *International*  
286 *journal of molecular sciences*. 2019;20(3):671. DOI: <https://dx.doi.org/10.3390/ijms20030671>
- 287 28. Rivas-San Vicente M, Plasencia J. Salicylic acid beyond defence: its role in plant growth and  
288 development. *Journal of experimental botany*. 2011;62(10):3321-3338. DOI:  
289 <https://dx.doi.org/10.1093/jxb/err031>
- 290 29. Manzoor K, Ilyas N, Batool N, Ahmad B, Arshad M. Effect of Salicylic Acid on the Growth and  
291 Physiological Characteristics of Maize under Stress Conditions. *Journal of the Chemical Society*  
292 *of Pakistan*. 2015;37(3).
- 293 30. Appu M, Muthukrishnan S. Foliar application of salicylic acid stimulates flowering and induce  
294 defense related proteins in finger millet plants. *Universal Journal of Plant Science*. 2014;2(1):14-  
295 18. DOI: <https://dx.doi.org/10.13189/ujps.2014.020102>
- 296 31. Xie Z, Zhang ZL, Hanzlik S, Cook E, Shen QJ. Salicylic acid inhibits gibberellin-induced alpha-  
297 amylase expression and seed germination via a pathway involving an abscisic-acid-inducible  
298 WRKY gene. *Plant molecular biology*. 2007;64:293-303. DOI: [https://dx.doi.org/10.1007/s11103-](https://dx.doi.org/10.1007/s11103-007-9152-0)  
299 [007-9152-0](https://dx.doi.org/10.1007/s11103-007-9152-0)
- 300 32. Sallam AM, Ibrahim HI. Effect of grain priming with salicylic acid on germination speed, seedling  
301 characters, anti-oxidant enzyme activity and forage yield of teosinte. *American-Eurasian Journal*  
302 *of Agricultural & Environmental Sciences*. 2015;15(5):744-753.
- 303 33. Vlot AC, Dempsey DM, Klessig DF. Salicylic acid, a multifaceted hormone to combat disease.  
304 *Annual review of phytopathology*. 2009;47:177-206. DOI:  
305 <https://dx.doi.org/10.1146/annurev.phyto.050908.135202>
- 306 34. Glazebrook J. Contrasting mechanisms of defense against biotrophic and necrotrophic  
307 pathogens. *Annual review of phytopathology*. 2005;43:205-227. DOI:  
308 <https://dx.doi.org/10.1146/annurev.phyto.43.040204.135923>
- 309 35. Jendoubi W, Harbaoui K, Hamada W. Salicylic acid-induced resistance against *Fusarium*  
310 *oxysporumf. s. pradicislycopercisi* in hydroponic grown tomato plants. *Journal of New Sciences*.  
311 2015;21.
- 312 36. Kundu S, Chakraborty D, Pal A. Proteomic analysis of salicylic acid induced resistance to  
313 Mungbean Yellow Mosaic India Virus in *Vigna mungo*. *Journal of proteomics*. 2011;74(3):337-349.  
314 DOI: <https://dx.doi.org/10.1016/j.jprot.2010.11.012>
- 315 37. Le Thanh T, Thumanu K, Wongkaew S, Boonkerd N, Teaumroong N, Phansak P, Buensanteai N.  
316 Salicylic acid-induced accumulation of biochemical components associated with resistance  
317 against *Xanthomonas oryzaepv. oryzae* in rice. *Journal of Plant Interactions*. 2017;12(1):108-120.  
318 DOI: <https://dx.doi.org/10.1080/17429145.2017.1291859>
- 319 38. Khanam NN, Ueno M, Kihara J, Honda Y, Arase S. Suppression of red light-induced resistance in  
320 broad beans to *Botrytis cinerea* by salicylic acid. *Physiological and molecular plant pathology*.  
321 2005;66(1-2):20-29. DOI: <https://dx.doi.org/10.1016/j.pmpp.2005.03.006>
- 322 39. Ferrari S, Plotnikova JM, De Lorenzo G, Ausubel FM. *Arabidopsis* local resistance to *Botrytis*  
323 *cinerea* involves salicylic acid and camalexin and requires *EDS4* and *PAD2*, but not *SID2*, *EDS5*

- 324 or *PAD4*. The Plant Journal. 2003;35(2):193-205. DOI: <https://dx.doi.org/10.1046/j.1365-313X.2003.01794.x>
- 325
- 326 40. Li L, Zou Y. Induction of disease resistance by salicylic acid and calcium ion against *Botrytis*
- 327 *cinerea* in tomato (*Lycopersicon esculentum*). Emirates Journal of Food and Agriculture. 2017;78-
- 328 82. DOI: <https://dx.doi.org/10.9755/ejfa.2016-10-1515>
- 329 41. Mohan Babu R, Sajeena A, Vijaya Samundeeswari A, Sreedhar A, Vidhyasekaran P,
- 330 Seetharaman K, Reddy MS. Induction of systemic resistance to *Xanthomonas oryzae* pv. *oryzae*
- 331 by salicylic acid in *Oryza sativa* (L.). Journal of Plant Diseases and Protection. 2003;110:419-431.
- 332 DOI: <https://dx.doi.org/10.1007/bf03356119>
- 333 42. Le Thanh T, Thumanu K, Wongkaew S, Boonkerd N, Teaumroong N, Phansak P, Buensanteai N.
- 334 Salicylic acid-induced accumulation of biochemical components associated with resistance
- 335 against *Xanthomonas oryzae* pv. *oryzae* in rice. Journal of Plant Interactions. 2017;12(1):108-120.
- 336 DOI: <https://dx.doi.org/10.1080/17429145.2017.1291859>
- 337 43. Daw BD, Zhang LH, Wang ZZ. Salicylic acid enhances antifungal resistance to *Magnaporthe*
- 338 *grisea* in rice plants. Australasian Plant Pathology. 2008;37:637-644. DOI:
- 339 <https://dx.doi.org/10.1071/AP08054>
- 340 44. Stella de Freitas TF, Stout MJ, Sant'Ana J. Effects of exogenous methyl jasmonate and salicylic
- 341 acid on rice resistance to *Oebalus pugnax*. Pest management science. 2019;75(3):744-752. DOI:
- 342 <https://dx.doi.org/10.1002/ps.5174>
- 343 45. Saikia R, Singh T, Kumar R, Srivastava J, Srivastava AK, Singh K, Arora DK. Role of salicylic acid
- 344 in systemic resistance induced by *Pseudomonas fluorescens* against *Fusarium oxysporum* f. sp.
- 345 *ciceri* in chickpea. Microbiological Research. 2003;158(3):203-213. DOI:
- 346 <https://dx.doi.org/10.1078/0944-5013-00202>
- 347 46. Connor D. Climate change and global crop productivity. Crop Science. 2002;42(3):978-979. DOI:
- 348 <https://dx.doi.org/10.2135/cropsci2002.9780>
- 349 47. Khan MI, Fatma M, Per TS, Anjum NA, Khan NA. Salicylic acid-induced abiotic stress tolerance
- 350 and underlying mechanisms in plants. Frontiers in plant science. 2015;6:135066. DOI:
- 351 <https://dx.doi.org/10.3389/fpls.2015.00462>
- 352 48. Horváth E, Csiszár J, Gallé Á, Poór P, Szepesi Á, Tari I. Hardening with salicylic acid induces
- 353 concentration-dependent changes in abscisic acid biosynthesis of tomato under salt stress.
- 354 Journal of Plant Physiology. 2015;183:54-63. DOI: <https://dx.doi.org/10.1016/j.jplph.2015.05.010>
- 355 49. Ali S, Ganai BA, Kamili AN, Bhat AA, Mir ZA, Bhat JA, Tyagi A, Islam ST, Mushtaq M, Yadav P,
- 356 Rawat S. Pathogenesis-related proteins and peptides as promising tools for engineering plants
- 357 with multiple stress tolerance. Microbiological research. 2018;212:29-37. DOI:
- 358 <https://dx.doi.org/10.1016/j.micres.2018.04.008>
- 359 50. Hong JK, Hwang BK. Induction of enhanced disease resistance and oxidative stress tolerance by
- 360 overexpression of pepper basic PR-1 gene in *Arabidopsis*. Physiologia Plantarum.
- 361 2005;124(2):267-277. DOI: <https://dx.doi.org/10.1111/j.1399-3054.2005.00515.x>
- 362 51. Sarowar S, Kim YJ, Kim EN, Kim KD, Hwang BK, Islam R, Shin JS. Overexpression of a pepper
- 363 basic pathogenesis-related protein 1 gene in tobacco plants enhances resistance to heavy metal

- 364 and pathogen stresses. Plant cell reports. 2005;24:216-224. DOI:  
365 <https://dx.doi.org/10.1007/s00299-005-0928-x>
- 366 52. Wu W, Ding YA, Wei W, Davis RE, Lee IM, Hammond RW, Zhao Y. Salicylic acid-mediated  
367 elicitation of tomato defence against infection by potato purple top phytoplasma. Annals of Applied  
368 Biology. 2012;161(1):36-45. DOI: <https://dx.doi.org/10.1111/j.1744-7348.2012.00550.x>
- 369 53. Wang W, Wang X, Huang M, Cai J, Zhou Q, Dai T, Cao W, Jiang D. Hydrogen peroxide and  
370 abscisic acid mediate salicylic acid-induced freezing tolerance in wheat. Frontiers in plant  
371 science. 2018;9:1137. DOI: <https://dx.doi.org/10.3389/fpls.2018.01137>
- 372 54. Krantev A, Yordanova R, Janda T, Szalai G, Popova L. Treatment with salicylic acid decreases the  
373 effect of cadmium on photosynthesis in maize plants. Journal of plant physiology.  
374 2008;165(9):920-931. DOI: <https://dx.doi.org/10.1016/j.jplph.2006.11.014>
- 375 55. Metwally A, Finkemeier I, Georgi M, Dietz KJ. Salicylic acid alleviates the cadmium toxicity in  
376 barley seedlings. Plant physiology. 2003;132(1):272-281. DOI:  
377 <https://dx.doi.org/10.1104/pp.102.018457>
- 378 56. Bandurska H, Stroi ski A. The effect of salicylic acid on barley response to water deficit. Acta  
379 Physiologiae Plantarum. 2005;27:379-386. DOI: <https://dx.doi.org/10.1007/s11738-005-0015-5>
- 380 57. Bulgarelli D, Rott M, Schlaeppi K, Ver Loren van Themaat E, Ahmadinejad N, Assenza F, Rauf P,  
381 Huettel B, Reinhardt R, Schmelzer E, Peplies J. Revealing structure and assembly cues for  
382 *Arabidopsis* root-inhabiting bacterial microbiota. Nature. 2012;488(7409):91-95. DOI:  
383 <https://dx.doi.org/10.1038/nature11336>
- 384 58. Lundberg DS, Lebeis SL, Paredes SH, Yourstone S, Gehring J, Malfatti S, Tremblay J,  
385 Engelbrekton A, Kunin V, Rio TG, Edgar RC. Defining the core *Arabidopsis thaliana* root  
386 microbiome. Nature. 2012;488(7409):86-90. DOI: <https://dx.doi.org/10.1038/nature11237>
- 387 59. Lebeis SL, Paredes SH, Lundberg DS, Breakfield N, Gehring J, McDonald M, Malfatti S, Glavina  
388 del Rio T, Jones CD, Tringe SG, Dangl JL. Salicylic acid modulates colonization of the root  
389 microbiome by specific bacterial taxa. Science. 2015;349(6250):860-864. DOI:  
390 <https://dx.doi.org/10.1126/science.aaa8764>
- 391 60. Zhu F, Fang Y, Wang Z, Wang P, Yang K, Xiao L, Wang R. Salicylic acid remodeling of the  
392 rhizosphere microbiome induces watermelon root resistance against *Fusarium oxysporum* f. sp.  
393 *niveum* infection. Frontiers in Microbiology. 2022;13:1015038. DOI:  
394 <https://dx.doi.org/10.3389/fmicb.2022.1015038>
- 395 61. Tamás L, Mistrík I, Alemayehu A, Zelinová V, Bočová B, Huttová J. Salicylic acid alleviates  
396 cadmium-induced stress responses through the inhibition of Cd-induced auxin-mediated reactive  
397 oxygen species production in barley root tips. Journal of Plant Physiology. 2015;173:1-8. DOI:  
398 <https://dx.doi.org/10.1016/j.jplph.2014.08.018>
- 399 62. Agtuca B, Rieger E, Hilger K, Song L, Robert CA, Erb M, Karve A, Ferrieri RA. Carbon-11 reveals  
400 opposing roles of auxin and salicylic acid in regulating leaf physiology, leaf metabolism, and  
401 resource allocation patterns that impact root growth in *Zea mays*. Journal of Plant Growth  
402 Regulation. 2014;33:328-339. DOI: <https://dx.doi.org/10.1007/s00344-013-9379-8>

- 403 63. Shakirova FM, Allagulova CR, Maslennikova DR, Klyuchnikova EO, Avalbaev AM, Bezrukova MV.  
404 Salicylic acid-induced protection against cadmium toxicity in wheat plants. *Environmental and*  
405 *experimental botany*. 2016;122:19-28. DOI: <https://dx.doi.org/10.1016/j.envexpbot.2015.08.002>
- 406 64. Per TS, Khan MI, Anjum NA, Masood A, Hussain SJ, Khan NA. Jasmonates in plants under  
407 abiotic stresses: Crosstalk with other phytohormones matters. *Environmental and experimental*  
408 *botany*. 2018;145:104-120. DOI: <https://dx.doi.org/10.1016/j.envexpbot.2017.11.004>
- 409 65. Sido KA, Hassan WA. Induction of defensive enzymes in sunflower plants treated with  
410 agrochemicals against *Macrophominaphaseolina*. *Journal of Plant Protection Research*.  
411 2022;34:1-9. DOI: <https://dx.doi.org/10.24425/jppr.2022.143233>
- 412 66. Petersen M, Brodersen P, Naested H, Andreasson E, Lindhart U, Johansen B, Nielsen HB, Lacy  
413 M, Austin MJ, Parker JE, Sharma SB. Arabidopsis MAP kinase 4 negatively regulates systemic  
414 acquired resistance. *Cell*. 2000;103(7):1111-1120. DOI: [https://dx.doi.org/10.1016/S0092-](https://dx.doi.org/10.1016/S0092-8674(00)00213-0)  
415 [8674\(00\)00213-0](https://dx.doi.org/10.1016/S0092-8674(00)00213-0)

UNDER PEER REVIEW