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**Abstract** Since ancient times, salicylic acid has been in use by humans because of its therapeutic properties. Salicylic acid, chemically known as 2-hydroxy benzoic acid is one of a diverse group of phenolic compounds, consisting of an aromatic ring bearing a hydroxyl group or its functional derivative, which is synthesized by plants. Salicylic acid biosynthetic pathway in plants has two distinct pathways, the isochorismate (IC) pathway and the phenylalanine ammonia-lyase (PAL) pathway. Moreover, salicylic acid plays exclusive role in plant growth, thermogenesis, flower induction and uptake of ions. It affects ethylene biosynthesis, stomatal movement and also reverses the effects of ABA on leaf abscission. In addition to this, it also enhances the level of photosynthetic pigments, photosynthetic rate and modifies the activity of some of the important enzymes as well. This chapter provides the reader with a comprehensive coverage to above aspects more exclusively with future prospects.

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**Keywords (separated by '-')** Growth - Photosynthesis - Salicylic acid - Senescence - Yield

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# Chapter 2

## Salicylic Acid: Physiological Roles in Plants

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Qazi Fariduddin and Aqil Ahmad

**Abstract** Since ancient times, salicylic acid has been in use by humans because of its therapeutic properties. Salicylic acid, chemically known as 2-hydroxy benzoic acid is one of a diverse group of phenolic compounds, consisting of an aromatic ring bearing a hydroxyl group or its functional derivative, which is synthesized by plants. Salicylic acid biosynthetic pathway in plants has two distinct pathways, the isochorismate (IC) pathway and the phenylalanine ammonia-lyase (PAL) pathway. Moreover, salicylic acid plays exclusive role in plant growth, thermogenesis, flower induction and uptake of ions. It affects ethylene biosynthesis, stomatal movement and also reverses the effects of ABA on leaf abscission. In addition to this, it also enhances the level of photosynthetic pigments, photosynthetic rate and modifies the activity of some of the important enzymes as well. This chapter provides the reader with a comprehensive coverage to above aspects more exclusively with future prospects.

**Keywords** Growth · Photosynthesis · Salicylic acid · Senescence · Yield

### 1 Introduction

Since ancient times, plants and their extracts have been used for their therapeutic properties. World Health Organization estimated that approximately 75–80 % of the world's population uses plant medicines either in part or entirely. Ancient

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25 Egyptians, for example, chewed willow bark to relieve fever and headaches.  
26 Thousands of years later, scientists discovered that the bark contains salicylic acid,  
27 the active ingredient used to make aspirin. In the year 1928, John Buchner isolated  
28 salicyl alcohol glucoside (Salicine) from willow bark that was later name as  
29 Salicylic Acid (hereafter SA) by Rafacle Piria in the year 1938.

30 SA, chemically known as 2-hydroxy benzoic acid is one of a diverse group of  
31 phenolic compounds, consisting of an aromatic ring bearing a hydroxyl group or  
32 its functional derivative, which is synthesized by plants. Plant phenolics were  
33 categorised as secondary metabolites and relatively treated as of low importance in  
34 plant metabolism but due to the passage of time this concept changed with the  
35 discovery that phenolics play important roles in plant metabolism. For example,  
36 phenolics are involved in lignin biosynthesis; others serve as allelopathic com-  
37 pounds, regulate plant responses to abiotic stimuli, or play critical roles in plant  
38 disease resistance either by functioning as preformed or inducible antimicrobial  
39 defence compounds termed phytoalexins or by signalling defence activation  
40 (Humphreys and Chapple 2002; Raskin 1992).

41 SA influences seed germination, seedling establishment, cell growth, respira-  
42 tion, stomatal closure, senescence-associated gene expression, basal thermotoler-  
43 ance, nodulation in legumes, and fruit yield (Vlot et al. 2009). The reason for some  
44 of these processes may be indirect because SA modulates the synthesis and/or  
45 signalling of other hormones such as jasmonic acid (hereafter JA), ethylene  
46 (hereafter ET), and auxin. It is ubiquitously distributed in the whole plant kingdom  
47 (Raskin et al. 1990a, b) and is categorised under group of Plant hormones (Raskin  
48 1992). Here, in this chapter, an effort has been made to insight into the the role of  
49 exogenously applied and/or endogenous SA in physiological and biochemical  
50 changes that occur in plants under normal conditions.

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## 51 2 Physiological Responses of SA

52 Plants have evolved some remarkable chemical substances, often to defend them-  
53 selves against being eaten. Among various phenolic substances, particularly SA  
54 exerts its influences on plant growth and development, photosynthetic machinery,  
55 flowering, membrane permeability, and enzyme activities. In this section we will  
56 learn about SA mediated physiological processes and try to elucidate the mecha-  
57 nisms behind the action of exogenously applied SA for growth and development.

### 58 2.1 Plant Growth and Development

59 Growth and development of plants, like all organisms, is regulated by various  
60 internal external stimuli. In recent years, SA has been in focus of intensive research  
61 due to its crucial role in the regulation of physiological and biochemical processes

62 during the entire life span of the plants and plays key roles in regulating their  
63 growth and productivity (Arberg 1981). The role of SA in seed germination has  
64 been debatable as there are inconsistent reports suggesting that it can either inhibit  
65 germination or increase seed vigour. The reported contradictory effects can be  
66 related to the SA concentrations employed. In *Arabidopsis thaliana*, SA concen-  
67 trations >1 mM delay or even inhibit germination (Rajou et al. 2006). In barley,  
68 doses >0.250 mM SA inhibit seed germination (Xie et al. 2007), while in maize  
69 germination is completely inhibited by SA doses ranging from 3 to 5 mM (Guan  
70 and Scandalios 1995). The effect of SA as a negative regulator of seed germination  
71 is probably due to an SA-induced oxidative stress. In *Arabidopsis* plants treated  
72 with SA (1–5 mM), hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>) levels increase up to 3-fold as a  
73 result of increased activities of Cu, Zn-superoxide dismutase and inactivation of the  
74 H<sub>2</sub>O<sub>2</sub>-degrading enzymes, catalase and ascorbate peroxidase (Rao et al. 1997).  
75 Enhanced germination and seedling growth were recorded in wheat, when the  
76 grains were subjected to pre-sowing seed-soaking treatment in SA (Shakirova  
77 2007). Fariduddin et al. (2003) reported that the dry matter accumulation was  
78 significantly enhanced in *Brassica juncea*, when lower concentrations of SA were  
79 sprayed. However, higher concentrations of SA had an inhibitory effect.

80 In another study, Hayat et al. (2005) showed that the leaf number, fresh and dry  
81 mass per plant of wheat seedlings raised from the grains soaked in lower con-  
82 centration (10<sup>-5</sup> M) of SA, increased significantly. Similar growth promoting  
83 responses were generated in barley seedlings sprayed with SA (Pancheva et al.  
84 1996). Khodary (2004) observed a significant increase in growth characteristics,  
85 pigment contents and photosynthetic rate in maize, sprayed with SA. The exog-  
86 enous SA application also enhanced the carbohydrate content in maize (Khodary  
87 2004). Hussein et al. (2007) in their pot experiment sprayed salicylic acid to the  
88 foliage of wheat plants, irrigated with Mediterranean sea water and reported an  
89 enhanced productivity due to an improvement in all growth characteristics  
90 including plant height, number and area of green leaves, stem diameter and dry  
91 weight of stem, leaves and of the plant as a whole.

92 In the year 1989, Carswell et al. reported that acetyl SA can promote colony  
93 formation in maize protoplasts suggesting a role for SA in the regulation of the cell  
94 cycle. xyloglucanendotransglucosylase/hydrolase (*XTH*) genes encode enzymes  
95 that are implicated in cell wall loosening and cell expansion (Rose et al. 2002).  
96 *Arabidopsis* contains 33 *XTH* genes in its genome (Yokoyama and Nishitani  
97 2001). Among 33 *XTH* genes, expression levels of *XTH8*, *XTH17* and *XTH31* were  
98 strongly down-regulated in both *cpr5* and *mpk4* but did not change in *nahG* (Miura  
99 et al. 2010). Reverse transcription-PCR (RT-PCR) results indicated that *XTH8*  
100 and *XTH31*, but not *XTH17*, were down-regulated in *siz1* and expression of  
101 *XTH8* and *XTH31* was recovered in *nahGsiz1-2* (Miura et al. 2010). Moreover,  
102 expression level of *XTH24* (MER15), a potential target for ANGUSTIFOLIA (*AN*),  
103 which regulates the width of leaves (Kim et al. 2002) and may also play a role in  
104 leaf morphogenesis at the early stage (Verica and Medford 1997). Thus, *SIZ1*  
105 regulates SA-dependent *XTH8* and *XTH31* expression, but may not be involved in  
106 AN-dependent regulation of cell elongation (Miura et al. 2010).

## 107 2.2 Photosynthetic Machinery

108 SA has been established as an important regulator of photosynthesis, water rela-  
 109 tions and metabolic aspects of plants, depending on its analogues, concentrations,  
 110 mode of application and plant type. SA is known to affect leaf and chloroplast  
 111 structure (Uzunova and Popova 2000), stomatal closure (Mateo et al. 2004;  
 112 Melotto et al. 2006), chlorophyll and carotenoid contents (Chandra and Bhatt  
 113 1998; Fariduddin et al. 2003), and the activity of enzymes such as RuBisCO  
 114 (ribulose-1,5-bisphosphate carboxylase/oxygenase) and carbonic anhydrase  
 115 (Slaymaker et al. 2002; Hayat et al. 2012; Yusuf et al. 2008, 2012). However, high  
 116 SA concentrations (1–5 mM) cause a reduction in the photosynthetic rate and  
 117 RuBisCO activity in barley plants (Pancheva et al. 1996), and reduce chlorophyll  
 118 contents in cowpea, wheat, and *Arabidopsis* (Rao et al. 1997; Chandra and Bhatt  
 119 1998; Moharekar et al. 2003). The decline of RuBisCO activity was attributed to a  
 120 50 % reduction in protein levels, compared with non-treated plants (Pancheva and  
 121 Popova 1998), while total soluble protein decreased by 68 %. Exogenously  
 122 applied SA induces alterations in leaf anatomy that consist of reduced width of the  
 123 adaxial and abaxial epidermis, and of the mesophyll tissue (Rivas-San Vicente and  
 124 Piasencia 2011). Such changes correlate ultrastructurally with an increase in  
 125 chloroplast volume, swelling of grana thylakoids, and coagulation of the stroma  
 126 (Uzunova and Popova 2000). Thus, the diminished photosynthetic activity at high  
 127 concentrations of SA is due to its effects on the thylakoid membranes and light-  
 128 induced reactions linked to them. Hayat et al. (2005) reported that the pigment  
 129 content was significantly enhanced in wheat seedlings, raised from the grains pre-  
 130 treated with lower concentration ( $10^{-5}$  M) of SA, whereas, higher concentrations  
 131 did not prove to be beneficial. Besides seed-soaking treatment, the foliar appli-  
 132 cation of SA also proved to be equally fruitful in increasing the pigment contents  
 133 in *Brassica napus* (Ghai et al. 2002). Similar results were obtained when the plants  
 134 of *Brassica juncea* were sprayed with lower concentration ( $10^{-5}$  M) of SA, where,  
 135 the chlorophyll content was significantly enhanced (Fariduddin et al. 2003).  
 136 Contrary to these observations, a reduction in chlorophyll content was observed in  
 137 plants pre-treated with SA (Anandhi and Ramanujam 1997; Pancheva et al. 1996).  
 138 Moharekar et al. (2003) reported that salicylic acid activated the synthesis of  
 139 carotenoids and xanthophylls and also enhanced the rate of de-epoxidation with a  
 140 concomitant decrease in chlorophyll pigments and chlorophyll a/b ratio in wheat  
 141 and moong. Exogenous application of SA enhanced the net photosynthetic rate,  
 142 internal CO<sub>2</sub> concentration, water use efficiency, stomatal conductance and trans-  
 143 piration rate in *Brassica juncea* (Fariduddin et al. 2003). Further, Khan et al.  
 144 (2003) reported an increase in transpiration rate and stomatal conductance in  
 145 response to foliar application of SA and other salicylates in corn and soybean. In  
 146 another study carried out on soybean, foliar application of salicylic acid enhanced  
 147 the water use efficiency, transpiration rate and internal CO<sub>2</sub> concentration (Kumar  
 148 et al. 2000).

149 However, contrary to these results, the transpiration rate decreased significantly  
150 in *Phaseolus vulgaris* and *Commelina communis* after the foliar application of SA  
151 and this decrease in transpiration rate was attributed to SA induced closure of  
152 stomata (Larque-Saavedra 1978, 1979; Khokon et al. 2010). Moreover, SA pre-  
153 treatment alleviated the loss of net photosynthetic rate under heat stress, apparently  
154 in part through maintaining a higher Rubisco activation state and greater PSII  
155 efficiency (Wang et al. 2010). SA also accelerated the increase of net photosyn-  
156 thetic rate mainly through the more rapid recovery of PSII function after heat  
157 stress and may be related to higher levels of HSP21 (Wang et al. 2010). Other  
158 mechanisms by which SA mediated protection of photosynthetic machinery are  
159 still to be determined.

### 160 2.3 Nitrate Metabolism

161 All the living organisms are basically composed of carbon, hydrogen, oxygen,  
162 nitrogen and minor quantities of other elements. These elements contribute to  
163 finally organize various biomolecules of the cell. Nitrogen is next to carbon in  
164 importance to living organisms. In a living cell, nitrogen is an important consti-  
165 tuent of amino acids, proteins, enzymes, vitamins, alkaloids and some growth  
166 hormones. Therefore, study of nitrogen metabolism is absolutely essential because  
167 the entire life process is dependent on these nitrogen-containing molecules. In this  
168 section, we will learn about various effects of SA on nitrogen metabolism  
169 including nitrogen fixation in plants. Nitrogen metabolism is an important aspect  
170 of legume-Rhizobium symbiosis. The exogenous SA affects the activities of the  
171 enzymes of nitrate/nitrogen metabolism as well. The activity of enzyme nitrate  
172 reductase (NR) was enhanced in the leaves of wheat following the exogenous  
173 application of SA. The treatment also protected the enzyme from the action of  
174 proteinases and trypsin (Rane et al. 1995). The total protein content was increased  
175 in soybean plants sprayed with SA and this increase might be due to enhanced  
176 activity of NR following the SA treatment (Kumar et al. 1999). A significant  
177 increase in the activity of nitrate reductase was observed both in roots and leaves  
178 of the plants raised from the wheat grains soaked in lower concentration ( $10^{-5}$  M)  
179 of SA (Hayat et al. 2005). Such a lower concentration of SA when sprayed to the  
180 foliage of mustard plants enhanced their NR activity (Fariduddin et al. 2003).  
181 However, at higher concentrations ( $10^{-3}$  or  $10^{-4}$  M), SA proved to be inhibitory.  
182 Mabood and Smith (2007) showed that exogenous SA inhibited the growth of  
183 Rhizobia and production of nod factors by them and also delayed the nodule  
184 formation, thereby decreasing the number of nodules per plant. However, SA level  
185 in the roots of *Medicago sativa*, inoculated with specific strain of *Rhizobia*, either  
186 decreased or remained close to the basal levels (Martinez-Abarca et al. 1998).  
187 Moreover, *Medicago sativa* plants when inoculated with an incompatible strain of  
188 *Rhizobia*, resulted in a marked accumulation of SA in the roots of host plant. It was



189 therefore, concluded that the compatible strains of *Rhizobia* produce certain  
 190 signals (specific nod factors) which are perceived by the host plant that suppress  
 191 the accumulation of SA in the roots (Martinez-Abarca et al. 1998).

192 Shah et al. (2001) reported that certain *Arabidopsis thaliana* mutants produce  
 193 elevated levels of SA and show constitutive expression of pathogenesis-related  
 194 genes and in some cases HR lesion formation even in the absence of pathogen  
 195 challenge. On the other hand, plants that express the bacterial *nahG* gene,  
 196 encoding salicylate hydroxylase, are unable to accumulate SA and are more sus-  
 197 ceptible to several pathogens (Gaffney et al. 1993). SA levels can also affect the  
 198 interaction of plants with symbiotic microorganisms. Medina et al. (2003) found  
 199 that *Nicotiana tabacum* plants expressing *NahG* had enhanced mycorrhizal fungal  
 200 infection, while plants constitutive for SA expression exhibited reduced infection.

201 Martinez-Abarca et al. (1998) showed SA accumulated in alfalfa roots, inoc-  
 202 ulated with a *nodC* mutant of *Sinorhizobium meliloti* that was unable to synthesize  
 203 the lipochitin nod signal required for infection. This report also showed that  
 204 exogenous addition of SA resulted in both reduced and delayed nodule formation  
 205 on alfalfa roots inoculated with wild-type *Sinorhizobium meliloti*. Subsequently,  
 206 Bueno et al. (2001) showed a decrease in antioxidant enzyme activities and an  
 207 increase in H<sub>2</sub>O<sub>2</sub> accumulation in alfalfa roots following inoculation with a  
 208 *Sinorhizobium meliloti nodC* mutant, as well as an increase in lipoxygenase  
 209 activity after inoculation with the wild-type strain.

210 Van Spronsen et al. (2003) reported that SA application inhibited indeterminate  
 211 nodulation of *Vicia sativa* but not determinate nodulation of *Lotus japonicus*. They  
 212 believed that fatty acid may be active in oxylipin signaling, which is known to be  
 213 inhibited by SA. Moreover, Rhizobia that form determinate nodules produce Nod  
 214 signals lacking poly-unsaturated fatty acids and thus, these signals may act in a  
 215 different way. However, the theory of van Spronsen et al. (2003) is inconsistent  
 216 with two reports showing that the addition of exogenous SA to *Glycine max*  
 217 seedlings inhibited early nodulation (Lian et al. 2000; Sato et al. 2002). *G. max*  
 218 forms determinate nodules.

## 219 2.4 Ethylene Production

220 The plant hormone, ethylene has been reported to affect a diverse array of plant  
 221 growth and developmental processes including germination, senescence and  
 222 abscission of flowers and leaves, fruit ripening as well as the response to a wide  
 223 variety of stresses such as pathogen attack and drought (Abeles et al. 1992). The  
 224 induction of ethylene biosynthesis takes place by a wide variety of stimuli,  
 225 including wounding, pathogen attack, various stresses, mechanical stimulus and by  
 226 hormones such as salicylic acid (Mattoo and Suttle 1991; Abeles et al. 1992;  
 227 Raskin 1992). Recently, the survey of literature revealed that SA has been shown  
 228 to interfere with the biosynthesis and/or action of ethylene in plants (Raskin 1992).  
 229 SA prevented the accumulation of ACC synthase transcripts induced by wounding

(Li et al. 1992) and inhibited ethylene synthesis in pear suspension cultures by blocking ACC oxidase (Szalai et al. 2000). SA can delay the ripening of banana fruit, probably through the inhibition of ethylene biosynthesis or its action (Srivastava and Dwivedi 2000). Both SA and its derivative acetyl salicylic acid (ASA) have been shown to inhibit ethylene production in cultured pear cells (Leslie and Romani 1986, 1988), mung bean hypocotyls, apple and pear fruit tissue discs (Romani et al. 1989), and carrot cell suspension cultures (Roustan et al. 1990). Fan et al. (1996) demonstrated the inhibitory action of SA on ACC oxidase activity in apple fruit discs. SA has also been shown to suppress lipoxygenase (LOX) activity in discs of kiwi fruit, with a consequent reduction in the production of free radicals and ethylene biosynthesis (Xu et al. 2000). There is evidence for a positive correlation between LOX activity and ethylene biosynthesis in apple fruit tissue (Marcelle 1991), and free radicals produced by LOX activity have been shown to play a role in regulating the biosynthesis of ethylene (Kacperska and Kubacka-Zebalska 1985, 1989), and in post-harvest ripening and softening of climacteric fruits such as apple (DePooter and Schamp 1989) and tomato (Todd et al. 1990). Moreover, an increase in endogenous ethylene biosynthesis at low concentrations of SA has been reported in suspension cultures of carrot (Nissen 1994) whereas, Srivastava and Dwivedi (2000) observed an inhibition of ethylene production at higher concentration ( $>10^{-4}$  M) of salicylic acid. However, it still remains unclear; the mechanism behind the action of SA mediated ethylene biosynthesis. Therefore, much debate is necessary to elucidate and pin point the mechanism associated with SA for ethylene biosynthesis and/or action.

## 2.5 Mineral Nutrients

Mineral nutrients are essential for growth and development of plants and microorganisms, as they are important factors in the regulation of various physiological and biochemical processes. How each element affects a plant's physiological and biochemical processes, (positively or negatively), is unique to each plant. This section briefly summarizes how different nutrients affect different plant's physiological processes in the presence of exogenous as well as endogenous salicylic acid. SA has an essential function in regulating plant developmental processes that affect nutrient uptake and their status; i.e. vascular differentiation, stem elongation, leaf development, and senescence (Rubio et al. 2009). However, a clear involvement of SA in the control of nutrient assimilation might be expected. Moreover, SA contributes in the control of redox status of plants, most likely by regulating the synthesis of the antioxidant glutathione, which protects plant against oxidative stress that follows many nutritional deficiencies (Freeman et al. 2005; Shao et al. 2007). Although these expectations, till now have no clear cut experimental evidence points to establish a relationship between SA signaling and the control of nutrient homeostasis. However comparisons among genes that respond to N-, K-, or S-limiting growth conditions with those altered by SA treatment

271 revealed a significant (positive or negative) correlation either for up or down  
 272 regulated genes. The uptake of phosphate (Glass 1973) and subsequently that of  
 273 potassium (Glass 1974) by barley roots was reduced by SA. However, the inhi-  
 274 bition of the absorption of potassium by oat roots, under the impact of SA, was  
 275 dependent on the pH and the concentration of the element in the medium. This  
 276 inhibition was more prominent at lower pH, suggesting higher activity of pro-  
 277 tonated form of salicylic acid (Harper and Balke 1981; Gordon et al. 2002). SA  
 278 also caused the collapse of the transmembrane electrochemical potential of  
 279 mitochondria and the ATP dependent proton gradient of tonoplast enriched vesi-  
 280 cles (Macri et al. 1986).

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## 281 2.6 Heat Production

282 Heat production, thermogenesis authenticates the discovery of SA as an endoge-  
 283 nous plant hormone. Initial findings proved that SA triggers a dramatic increase in  
 284 the production of metabolic heat and insect-attracting chemicals in the thermo-  
 285 genic inflorescence of *Arum lilies* (Raskin 1992) and possibly other plants also  
 286 (Raskin et al. 1990a, b). In *Sauromatum guttatum* Schott (voodoo lily), a 100-fold  
 287 increase in SA precedes with the onset of thermogenesis in the spadix (Vlot et al.  
 288 2009). The induction of thermogenesis by SA is very specific: of 33 SA analogues  
 289 tested, only 2, 6-dihydroxybenzoic acid and aspirin induce this response. SA  
 290 stimulates thermogenesis primarily by increasing the activity of alternative  
 291 respiratory pathway in mitochondria. Unlike the cytochrome respiratory pathway,  
 292 electron flow through the alternative respiratory pathway generates ATP at only  
 293 one site with the unused potential energy being released as heat (Vlot et al. 2009).  
 294 Remarkably, SA treatment also induces alternative oxidase expression and  
 295 increased alternative respiration in tobacco, a nonthermogenic plant (Norman et al.  
 296 2004). Exogenously applied SA treatment improved thermotolerance and heat  
 297 acclimation in mustard seedlings (Dat et al. 1998). A similar response was also  
 298 observed in potato plantlets, raised from the cultures, supplemented with lower  
 299 concentrations of acetyl salicylic acid (Lopez-Delgado et al. 1998). Larkindale and  
 300 Huang (2004) pointed out that the enhanced heat tolerance in plants of *Agrostis*  
 301 *stolonifera*, pre-treated with salicylic acid was due to the protection of plants from  
 302 oxidative damage. These authors further reported that the pre-treatment with  
 303 salicylic acid had no effect on POX activity, whereas, the CAT activity declined,  
 304 compared to control. Foliar spray of lower concentrations of salicylic acid con-  
 305 ferred heat tolerance to mustard. Further this treatment accompanied with hard-  
 306 ening at 45 °C for 1 h enhanced H<sub>2</sub>O<sub>2</sub> level and also reduced CAT activity,  
 307 thereby increasing the potential of plants to withstand the heat stress (Dat et al.  
 308 1998).

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309

## 2.7 Flowering

310 Plant reproduction relies on the successful flowering at the required season and  
311 developmental stage. Studies in *Arabidopsis thaliana* revealed that endogenous  
312 factors that affect flowering involved autonomous gibberellin pathways (Blazquez  
313 et al. 1998); Koornneef et al. 1998; Wilson et al. 1992). As a result, mechanisms  
314 have been evolved that integrate environmental signals with endogenous devel-  
315 opmental signals to regulate flowering time (Simpson and Dean 2002). The pos-  
316 sibility of SA being an endogenous plant signal was first raised by Cleland and co-  
317 workers (Raskin 1992). Moreover, the very first physiological symptom, ever  
318 accredited to SA in plants, was its impact on flower induction in tobacco tissue  
319 culture, supplemented with kinetin and indole acetic acid (Lee and Skoog 1965;  
320 Eberhard et al. 1989). In addition to this, analyzing different fractions of honeydew  
321 collected from aphids feeding on vegetative or flowering *Xanthium strumarium*,  
322 they identified SA as a phloem mobile activity capable of inducing flowering in  
323 *Lemna gibba* (Vlot et al. 2009). The study of Khurana and Cleland (1992) revealed  
324 that *Lemna paucicostata* LP6 does not normally flower when grown on basal  
325 Bonner-Devirian medium, but substantial flowering is obtained when 10  $\mu\text{M}$   
326 salicylic acid (SA) or benzoic acid is added to the medium. Moreover, Wada et al.  
327 (2010) showed that poor-nutrition stress induced flowering was inhibited by  
328 amino-oxy acetic acid, a phenylalanine ammonia lyase inhibitor, and this inhibi-  
329 tion was almost completely reversed by salicylic acid (SA). However, exogenously  
330 applied SA did not induce flowering under non-stress conditions, suggesting that  
331 SA may be necessary but not sufficient to induce flowering. Different plant species  
332 including ornamental plant *Sinningia speciosa* flowered much earlier as compared  
333 to the untreated control, on receiving an exogenous foliar spray of salicylic acid  
334 (Martin-Mex et al. 2003, 2005a, b). Promising results were obtained when plants  
335 of *Carica papaya* were treated with salicylic acid which showed a significantly  
336 higher fruit set (Herrera-Tuz 2004; Martin-Mex et al. 2005a, b). In cucumber and  
337 tomato, the fruit yield enhanced significantly when the plants were sprayed with  
338 lower concentrations of salicylic acid (Larque-Saavedra and Martin-Mex 2007).  
339 Moreover, Alaey et al. (2011) reported that SA has the ability to increase the vase-  
340 life of cut rose flowers and delay senescence by regulating plant water content and  
341 increasing the scavenging capacity of cells. However, the recent demonstrations  
342 revealed that (a) SA-deficient *Arabidopsis* failed to initiate flowering in response  
343 to UV-C irradiation and flowered substantially later than wild-type (wt) plants  
344 when grown under non-stress conditions and (b) SIZ1, a SUMO E3 ligase, neg-  
345 atively regulates flowering via SA-dependent pathway argue that SA plays some  
346 role in this process.

347 **2.8 Senescence**

348 Plant senescence is a phenomenon that resembles age of the plant that closely  
349 connects with cell death. It is developmentally well defined that optimizes the  
350 growth and reproductive capacity of plants by recycling of resources from  
351 senescing leaves into young leaves or seeds. After well documented the impor-  
352 tance of role of SA in photosynthesis and flowering, it is not unanticipated that this  
353 plant hormone is also involved in regulation of senescence. This process is  
354 characterized by yellowing of leaves due to chlorophyll degradation (Vogelmann  
355 et al. 2012) and increased ROS levels (Rivas-San and Plasencia 2011). It is  
356 believed that these events are due to SA accumulation. In *Arabidopsis* senescent  
357 leaves, SA levels increase 4-fold at the mid-senescent stage. Consistent with this  
358 observation, *Arabidopsis* plants affected in SA biosynthesis, such as the transgenic  
359 NahG and the mutant pad4, or with a disrupted SA signalling pathway, such as  
360 npr1, exhibit altered senescence patterns that include delayed yellowing and  
361 reduced necrosis compared with wild-type plants (Morris et al. 2000). Moreover,  
362 senescence is escorted by important changes in gene expression, and SA paly  
363 pivotal role in successful execution of this process. Transcripts of several SAGs,  
364 such as *SAG12*, are considerably reduced or undetectable in SA-deficient *Ara-*  
365 *bidopsis* plants (Morris et al. 2000). In addition this, SA activates the expression of  
366 the *Arabidopsis* senescence-related genes  $\alpha$ VPE,  $\gamma$ VPE, *WRKY6*, *WRKY53*, and  
367 *SEN1* that encode two vacuolar processing enzymes, two transcription factors, and  
368 a protease, respectively (Robatzek and Somssich 2001; Miao et al. 2004; Schenk  
369 et al. 2005). The involvement of the SA signalling pathway in senescence was  
370 confirmed through a detailed microarray analysis in *Arabidopsis* senescent leaves  
371 (Buchanan-Wollaston et al. 2005). Almost 20 % of the up-regulated genes during  
372 senescence show at least 2-fold reduced expression in SA-deficient NahG trans-  
373 genic plants. Most of the senescence enhanced genes that are dependent on the SA  
374 pathway encode kinases, transferases, and hydrolases, but their function in  
375 senescence progression remains to be elucidated. Although a great deal of effort  
376 has been put into identifying the signalling factors required for senescence regu-  
377 lation, further research must determine whether SA is involved in different stages  
378 of senescence, and the interconnecting networks with other phytohormones that  
379 promote (ABA, JA, an ET) or delay (CKs and GAs) senescence.

380 **3 Effect of SA on Yield**

381 The credibility on any exogenously sourced plant hormones evaluate in terms of  
382 biological yield. SA is known to be a natural signal molecule has been shown to  
383 play an important role in regulating various physiological processes in plants  
384 including yield. Yildirim and Dursan (2009) revealed that foliar application of SA  
385 showed positive effect on early yield and total yield and also proposed that highest



386 yield occurred in 0.50 mM SA treatment and also recommended in order to  
387 improve yield. Sharafizad et al. (2012) showed that highest grain yield was  
388 obtained with application of 0.07 mmol SA. It is believed that increasing the crop  
389 yield might be due to delayed senescence of plant organs (particularly leaves and  
390 flowers) in response to exogenous SA (Imran et al. 2007) that will automatically  
391 help the plant in extending the duration of photosynthetically active sites and also  
392 prevent the premature loss of flowers and fruits. This consequently resulted in the  
393 observed increase in the number of crop yield. Moreover, Marschner (2003) that  
394 phytohormones increase the degree of sink at the level of seeds, directing the flow  
395 of metabolites to the developing seeds consequent to an improvement in the seed  
396 mass and seed yield per plant at harvest.

## 397 4 Conclusions

398 Much has been debated during the last decades regarding the applicability of SA as  
399 plant hormone by exploring its morpho-physiological responses under exogenous  
400 application. This review article showed that much progress has been achieved in  
401 the biosynthesis and metabolism of SA, whereas it is the need of time to focus to  
402 identify and characterize SA biosynthetic with involved enzymes and also isolate  
403 their genes. Better understanding of SA biosynthesis and metabolism may improve  
404 the plant resistance to pathogens, in the future by providing the tools necessary to  
405 manipulate endogenous as well as exogenous levels of SA. Moreover, biggest  
406 concern regarding SA mediated response is that how SA triggers such responses  
407 effectively and exactly and the mechanism related to it. In addition to this, it is also  
408 necessary to reveal how SA negatively and positively interacts with several other  
409 plant hormones and signaling molecules that not only affect defense but also  
410 regulate developmental processes. An ongoing challenge is to unravel how these  
411 interactions affect different processes that are occurring in parallel.

## 412 References

- 413 Abeles, F. B., Morgan, P. W., & Saltveit, J. M. E. (1992). *Ethylene in plant biology* (2nd ed.). San  
414 Diego: Academic Press.
- 415 Alaei, M., Babalar, M., Naderi, R., & Kafi, M. (2011). Effect of pre- and postharvest salicylic  
416 acid treatment on physio-chemical attributes in relation to vase-life of rose cut flowers.  
417 *Postharvest Biology and Technology*, 61, 91–94.
- 418 Anandhi, S., & Ramanujam, M. P. (1997). Effect of salicylic acid on black gram (*Vigna mungo*)  
419 cultivars. *Industrial Journal of Plant Physiology*, 2, 138–141.
- 420 Arberg, B. (1981). Plant growth regulators. Monosubstituted benzoic acid. *Swedish Agriculture*  
421 *Research*, 11, 93–105.
- 422 Blazquez, M. A., Green, R., Nilsson, O., Sussman, M. R., & Weigel, D. (1998). Gibberellins  
423 promote flowering of Arabidopsis by activating *LEAFY* promoter. *Plant Cell*, 10, 791–800.

- 424 Buchanan-Wollaston, V., Page, T., Harrison, E., Breeze, E., Lim, P. O., Nam, H. G., et al. (2005).  
425 Comparative transcriptome analysis reveals significant differences in gene expression and  
426 signalling pathways between developmental and dark/starvation-induced senescence in  
427 *Arabidopsis*. *The Plant Journal*, *42*, 567–585.
- 428 Bueno, P., Soto, M. J., Rodríguez-Rosales, M. P., Sanjuan, J., Olivares, J., & Donaire, J. P.  
429 (2001). Time-course lipoxygenase, antioxidant enzyme activities and H<sub>2</sub>O<sub>2</sub> accumulation  
430 during the early stages of Rhizobium-legume symbiosis. *New Phytologist*, *152*, 91–96.
- 431 Carswell, G. K., Johnson, C. M., Shillito, R. D., & Harms, C. T. (1989). O-acetyl-salicylic acid  
432 promotes colony formation from protoplasts of an elite maize inbred. *Plant Cell Reports*, *8*,  
433 282–284.
- 434 Chandra, A., & Bhatt, R. K. (1998). Biochemical and physiological response to salicylic acid in  
435 relation to the systemic acquired resistance. *Photosynthetica*, *35*, 255–258.
- 436 Dat, J. F., Lopez-Delgado, H., Foyer, C. H., & Scott, I. M. (1998). Parallel changes in H<sub>2</sub>O<sub>2</sub> and  
437 catalase during thermotolerance induced by salicylic acid or heat acclimation in mustard  
438 seedlings. *Plant Physiology*, *116*, 1351–1357.
- 439 De-Pooter, H. L., & Schamp, N. M. (1989). Involvement of lipoxygenase-mediated lipid  
440 catabolism in the start of the autocatalytic ethylene production by apples (cv. Golden  
441 Delicious): a ripening hypothesis. *Acta Horticulturae*, *258*, 47–53.
- 442 Eberhard, S., Doubra, N., Marta, V., Mohnen, D., Southwick, A., Darvill, A., et al. (1989).  
443 Pectic cell wall fragments regulate tobacco thin cell layer explant morphogenesis. *Plant Cell*,  
444 *1*, 747–755.
- 445 Fan, X., Mattheis, J. P., & Fellman, J. K. (1996). Inhibition of apple fruit 1-amino cyclopropane-  
446 1-carboxylic acid oxidase activity and respiration by acetyl salicylic acid. *Journal of Plant*  
447 *Physiology*, *149*, 469–471.
- 448 Fariduddin, Q., Hayat, S., & Ahmad, A. (2003). Salicylic acid influences net photosynthetic rate,  
449 carboxylation efficiency, nitrate reductase activity, and seed yield in *Brassica juncea*.  
450 *Photosynthetica*, *41*, 281–284.
- 451 Freeman, J. L., Garcia, D., Kim, D., Hopf, A., & Salt, D. E. (2005). Constitutively elevated  
452 salicylic acid signals glutathione-mediated nickel tolerance in *Thlaspi* nickel hyperaccumu-  
453 lators. *Plant Physiology*, *137*, 1082–1091.
- 454 Gaffney, T., Friedrich, L., Vernooij, B., Negrotto, D., Nye, G., Uknes, S., et al. (1993).  
455 Requirement of salicylic acid for the induction of systemic acquired resistance. *Science*, *261*,  
456 754–756.
- 457 Ghai, N., Setia, R. C., & Setia, N. (2002). Effects of paclobutrazol and salicylic acid on  
458 chlorophyll content, hill activity and yield components in *Brassica napus* L. (cv. GSL-1).  
459 *Phytomorphol*, *52*, 83–87.
- 460 Glass, A. D. (1973). Influence of phenolic acids on ion uptake. I. Inhibition of phosphate uptake.  
461 *Plant Physiology*, *51*, 1037–1041.
- 462 Glass, A. D. (1974). Influence of phenolic acids upon ion uptake. III. Inhibition of potassium  
463 absorption. *Journal of Experimental Botany*, *25*, 1104–1113.
- 464 Gordon, L. K., Minibayeva, F. V., Ogerodnikova, T. I., Rakhmatullina, D. F., Tzentzevitzky, A.  
465 N., Maksyutin, D. A., et al. (2002). Salicylic acid induced dissipation of the proton gradient on  
466 the plant cell membrane. *Doklady Biology Science*, *387*, 581–583.
- 467 Guan, L., & Scandalios, J. G. (1995). Developmentally related responses of maize catalase genes  
468 to salicylic acid. *Proceedings of National Academy of Science. USA*, *92*, 5930–5934.
- 469 Harper, J. P., & Balke, N. E. (1981). Characterization of the inhibition of K<sup>+</sup> absorption in oat  
470 roots by salicylic acid. *Plant Physiology*, *68*, 1349–1353.
- 471 Hayat, S., Fariduddin, Q., Ali, B., & Ahmad, A. (2005). Effect of salicylic acid on growth and  
472 enzyme activities of wheat seedlings. *Acta Agronomica Hungarica*, *53*, 433–437.
- 473 Hayat, Q., Hayat, S., Alyemini, M. N., & Ahmad, A. (2012). Salicylic acid mediated changes in  
474 growth, photosynthesis, nitrogen metabolism and antioxidant defense system in *Cicer*  
475 *arietinum* L. *Plant Soil Environment*, *58*, 417–423.

- 476 Herrera-Tuz, R. (2004). Reguladores de crecimiento XXI. Efecto del ácido salicílico en la  
477 productividad de papaya maradol (Carica papaya L.). Tesis de Licenciatura. Instituto  
478 Tecnológico Agropecuario, Conkal, Yucatán, México.
- 479 Humphreys, J. M., & Chapple, C. (2002). Rewriting the lignin roadmap. *Current Opinion in*  
480 *Plant Biology*, 5, 224–229.
- 481 Hussein, M. M., Balbaa, L. K., & Gaballah, M. S. (2007). Salicylic Acid and Salinity Effects on  
482 Growth of Maize Plants. *Research Journal Agricultural Biology Science*, 3, 321–328.
- 483 Imran, H., Zhang, Y., Du, G., Wang, G., & Zhang, J. (2007). Effect of Salicylic Acid (SA) on  
484 delaying fruit senescence of Huang Kum pear. *Front Agric China*, 1, 456–459.
- 485 Kacperska, A., & Kubacka-Zebalska, M. (1989). Formation of stress ethylene depends both on  
486 ACC synthesis and on the activity of free radical-generating system. *Physiologia Plantarum*,  
487 77, 231–237.
- 488 Kacperska, A., & Ku-Zebalska, M. (1985). Is lipoxygenase involved in the formation of ethylene  
489 from ACC? *Physiologia Plantarum*, 64, 333–338.
- 490 Khan, W., Prithviraj, B., & Smith, D. L. (2003). Photosynthetic responses of corn and soybean to  
491 foliar application of salicylates. *Journal of Plant Physiology*, 160, 485–492.
- 492 Khodary, S. F. A. (2004). Effect of salicylic acid on the growth, photosynthesis and carbohydrate  
493 metabolism in salt stressed maize plants. *International Journal of Agriculture Biology*, 6, 5–8.
- 494 Khokon, M. A. R., Hossain, M. A., Munemasa, S., Uraji, M., Nakamura, Y., Mori, I. C., et al.  
495 (2010). Yeast elicitor-induced stomatal closure and peroxidase-mediated ROS production in  
496 *Arabidopsis*. *Plant and Cell Physiology*, 51, 1915–1921.
- 497 Khurana, J. P., & Cleland, C. F. (1992). Role of salicylic acid and benzoic acid in flowering of a  
498 photoperiod-insensitive strain, *Lemna paucicostata* LP6. *Plant Physiology*, 100, 1541–1546.
- 499 Kim, G. T., Shoda, K., Tsuge, T., Cho, K. H., Uchimiyama, H., Yokoyama, R., et al. (2002). The  
500 *ANGUSTIFOLIA* gene of *Arabidopsis*, a plant CtBP gene, regulates leaf-cell expansion, the  
501 arrangement of cortical microtubules in leaf cells and expression of a gene involved in cell-  
502 wall formation. *EMBO Journal*, 21, 1267–1279.
- 503 Koornneef, M., Alonso-Blanco, C., Peeters, A. J. M., & Soppe, W. (1998). Genetic control of  
504 flowering time in *Arabidopsis*. *Annual Review Plant Physiology. Plant Molecular Biology*, 49,  
505 345–370.
- 506 Kumar, P., Dube, S. D., & Chauhan, V. S. (1999). Effect of salicylic acid on growth, development  
507 and some biochemical aspects of soybean (*Glycine max* L. Merrill). *Industrial Journal Plant*  
508 *Physiology*, 4, 327–330.
- 509 Kumar, P., Lakshmi, N. J., & Mani, V. P. (2000). Interactive effects of salicylic acid and  
510 phytohormones on photosynthesis and grain yield of soybean (*Glycine max* L. Merrill).  
511 *Physiology Molecular Biology of Plants*, 6, 179–186.
- 512 Larkindale, J., & Huang, B. (2004). Thermotolerance and antioxidant systems in *Agrostis*  
513 *stolonifera*: Involvement of salicylic acid, abscisic acid, calcium, hydrogen peroxide, and  
514 ethylene. *Journal of Plant Physiology*, 161, 405–413.
- 515 Larqué-Saavedra, A. (1978). The anti-transpirant effect of acetylsalicylic acid on *Phaseolus*  
516 *vulgaris* L. *Physiologia Plantarum*, 43, 126–128.
- 517 Larqué-Saavedra, A. (1979). Stomatal closure in response to acetylsalicylic acid treatment.  
518 *Zeitschrift für Pflanzenphysiologie*, 93, 371–375.
- 519 Larqué-Saavedra, A., & Martín-Mex, F. (2007). Effects of salicylic acid on the bioproductivity of  
520 the plants. In S. Hayat & A. Ahmad (Eds.), *Salicylic Acid, a Plant Hormone*. Dordrecht:  
521 Springer.
- 522 Lee, T. T., & Skoog, F. (1965). Effect of substituted phenols on bud formation and growth of  
523 tobacco tissue culture. *Physiologia Plantarum*, 18, 386–402.
- 524 Leslie, C. A., & Romani, R. J. (1986). Salicylic acid: a new inhibitor of ethylene biosynthesis.  
525 *Plant Cell Reports*, 5, 144–146.
- 526 Leslie, C. A., & Romani, R. J. (1988). Inhibition of ethylene biosynthesis by salicylic acid. *Plant*  
527 *Physiology*, 88, 833–837.



- 528 Li, N., Parsons, B. L., Liu, D., & Mattoo, A. K. (1992). Accumulation of wound-inducible ACC  
529 synthase transcript in tomato fruit is inhibited by salicylic acid and polyamines. *Plant*  
530 *Molecular Biology*, *18*, 477–487.
- 531 Lian, B., Zhou, X., Miransari, M., & Smith, D. L. (2000). Effects of salicylic acid on the  
532 development and root nodulation of soybean seedlings. *Journal of Agronomy and Crop*  
533 *Science*, *185*, 187–192.
- 534 Lopez-Delgado, H., Dat, J. F., Foyer, C. H., & Scott, I. M. (1998). Induction of thermotolerance  
535 in potato microplants by acetylsalicylic acid and H<sub>2</sub>O<sub>2</sub>. *Journal of Experimental Botany*, *49*,  
536 713–720.
- 537 Mabood, F., & Smith, D. (2007). The role of salicylates in rhizobium-legume symbiosis and  
538 abiotic stresses in higher plants. In S. Hayat & A. Ahmad (Eds.), *Salicylic acid: A plant*  
539 *hormone* (pp. 151–162). Dordrecht: Springer.
- 540 Marcelle, R. D. (1991). Relationship between mineral content, lipooxygenase activity, levels of  
541 1-aminocyclopropane carboxylic acid and ethylene emission in apple fruit flesh disks (cv.  
542 Jonagold) during storage. *Postharvest Biology and Technology*, *1*, 101–109.
- 543 Marschner, H. (2003). *Mineral nutrition of higher plants* (3rd ed.). London: Academic Press.
- 544 Martinez-Abarca, F., Herrera-Cervara, J. A., Bueno, P., Sanjuan, J., Bisseling, T., & Olivares, J.  
545 (1998). Involvement of salicylic acid in the establishment of the *Rhizobium meliloti*-alfalfa  
546 symbiosis. *Molecular Plant-Microbe Interaction*, *11*, 153–155.
- 547 Martin-Mex, R., Villanueva-Couoh, E., Uicab-Quijano, V., and Larque-Saavedra, A. (2003).  
548 Positive effect of salicylic acid on the flowering of gloxinia. In: Proceedings 31st Annual  
549 Meeting. Plant Growth Regulatory Society America, Canada: Vancouver (pp 149–151),  
550 August 3–6 2003
- 551 Martin-Mex, R., Nexticapan-Garces, A., and Larque-Saavedra, A. (2005a). Effect of salicylic  
552 acid in sex expression in *Carica papaya* L. In: 10th International Symposium on Plant  
553 Biorregulators in Fruit Production, Mexico (p. 113), June 26–30.
- 554 Martin-Mex, R., Villanueva-Couoh, E., Herrera-Campos, T., & Larque-Saavedra, A. (2005b).  
555 Positive effect of salicylates on the flowering of African violet. *Science Horticulture*, *103*,  
556 499–502.
- 557 Mateo, A., Muhlenbock, P., Rusterucci, C., Chang, C. C., Miszalski, Z., Karpinska, B., et al.  
558 (2004). Lesion Simulating Disease 1 is required for acclimation to conditions that promote  
559 excess excitation energy. *Plant Physiology*, *136*, 2818–2830.
- 560 Mattoo, A. K., & Suttle, J. C. (1991). *The plant hormone ethylene*. Boca Raton: CRC Press.
- 561 Medina, M. J. H., Gagnon, H., Piche, Y., Ocampo, J. A., Garrido, J. M. G., & Vierheilig, H.  
562 (2003). Root colonization by arbuscular mycorrhizal fungi is affected by the salicylic acid  
563 content of the plant. *Plant Science*, *164*, 993–998.
- 564 Mehran, S., Ahmad, N., Seyed, A. S., Tayeb, S., & Shahram, Lak. (2012). Effect of salicylic acid  
565 pretreatment on yield, its components and remobilization of stored material of wheat under  
566 drought stress. *Journal of Agricultural Science*, *4*, 10.
- 567 Melotto, M., Underwood, W., Koczan, J., Nomura, K., & He, S. Y. (2006). Plant stomata function  
568 in innate immunity against bacterial invasion. *Cell*, *126*, 969–980.
- 569 Miao, Y., Laun, T., Zimmermann, P., & Zentgraf, U. (2004). Targets of the WRKY53  
570 transcription factor and its role during leaf senescence in *Arabidopsis*. *Plant Molecular*  
571 *Biology*, *55*, 853–867.
- 572 Miura, K., Lee, J., Miura, T., & Hasegawa, P. M. (2010). SIZ1 controls cell growth and plant  
573 development in *Arabidopsis* through salicylic acid. *Plant and Cell Physiology*, *51*, 103–113.
- 574 Moharekar, S. T., Lokhande, S. D., Hara, T., Tanaka, R., Tanaka, A., & Chavan, P. D. (2003).  
575 Effects of salicylic acid on chlorophyll and carotenoid contents on wheat and moong  
576 seedlings. *Photosynthetica*, *41*, 315–317.
- 577 Morris, K., MacKerness, S. A., Page, T., John, C. F., Murphy, A. M., Carr, J. P., et al. (2000).  
578 Salicylic acid has a role in regulating gene expression during leaf senescence. *Plant Journal*,  
579 *23*, 677–685.
- 580 Nissen, P. (1994). Stimulation of somatic embryogenesis in carrot by ethylene: Effects of  
581 modulators of ethylene biosynthesis and action. *Physiologia Plantarum*, *92*, 397–403.

- 582 Norman, C., Howell, K. A., Millar, A. H., Whelan, A. H., & Day, D. A. (2004). Salicylic acid is an  
583 uncoupler and inhibitor of mitochondrial electron transport. *Plant Physiology*, *134*, 492–501.
- 584 Pancheva, T. V., & Popova, L. P. (1998). Effect of the salicylic acid on the synthesis of ribulose-  
585 1,5-bisphosphate carboxylase/oxygenase in barley leaves. *Plant Physiology*, *152*, 381–386.
- 586 Pancheva, T. V., Popova, L. P., & Uzunova, A. M. (1996). Effect of salicylic acid on growth and  
587 photosynthesis in barley plants. *Journal of Plant Physiology*, *149*, 57–63.
- 588 Rajou, L., Belghazi, M., Huguet, R., Robin, C., Moreau, A., Job, C., et al. (2006). Proteomic  
589 investigation of the effect of salicylic acid on Arabidopsis seed germination and establishment  
590 of early defense mechanisms. *Plant Physiology*, *141*, 910–923.
- 591 Rane, J., Lakkineni, K. C., Kumar, P. A., & Abrol, Y. P. (1995). Salicylic acid protects nitrate  
592 reductase activity of wheat leaves. *Plant Physiology and Biochemistry*, *22*, 119–121.
- 593 Rao, M. V., Paliyath, G., Ormrod, D. P., Murr, D. P., & Watkins, C. B. (1997). Influence of  
594 salicylic acid on H<sub>2</sub>O<sub>2</sub> production, oxidative stress, and H<sub>2</sub>O<sub>2</sub>-metabolizing enzymes. *Plant*  
595 *Physiology*, *115*, 137–149.
- 596 Raskin, I. (1992). Role of salicylic acid in plants. *Annual Review Plant Physiology*, *43*, 439–463.
- 597 Raskin, I., Skubatz, H., Tang, W., & Meeuse, B. J. D. (1990a). Salicylic acid levels in  
598 thermogenic and nonthermogenic plants. *Annals of Botany*, *66*, 376–383.
- 599 Raskin, I., Skubatz, H., Tang, W., & Meeuse, B. J. D. (1990b). Salicylic acid levels in  
600 thermogenic and non-thermogenic plants. *Annals of Botany*, *66*, 369–373.
- 601 Rivas-San, V., & Plasencia, J. (2011). Salicylic acid beyond defence: its role in plant growth and  
602 development. *Journal of Experimental Botany*, *62*, 3321–3338.
- 603 Robatzek, S., & Somssich, E. (2001). A new member of the *Arabidopsis* WRKY transcription  
604 factor family, *AtWRKY6*, is associated with both senescence-and defence-related processes.  
605 *The Plant Journal*, *28*, 123–133.
- 606 Romani, R. J., Hess, B. M., & Leslie, C. A. (1989). Salicylic acid inhibition of ethylene production  
607 by apple discs and other plant tissues. *Journal of Plant Growth Regulation*, *8*, 63–69.
- 608 Rose, J. K. C., Braam, J., Fry, S. C., & Nishitani, K. (2002). The XTH family of enzymes  
609 involved in xyloglucan endotransglucosylation and endohydrolysis: Current perspectives and  
610 a new unifying nomenclature. *Plant and Cell Physiology*, *43*, 1421–1435.
- 611 Roustan, J. P., Latche, A., & Fallot, J. (1990). Inhibition of ethylene production and stimulation  
612 of carrot somatic embryogenesis by salicylic acid. *Biologia Plantarum*, *32*, 273–276.
- 613 Rubio, J. S., Garcia-Sanchez, F., Rubio, F., & Martinez, V. (2009). Yield, blossom end rot  
614 incidence, and fruit quality in pepper plants under moderate salinity are affected by K<sup>+</sup> and  
615 Ca<sup>2+</sup> fertilization. *Scientia Horticulturae*, *119*, 79–87.
- 616 Ryals, J. A., Neuenschwander, U. H., Willits, M. G., Molina, A., Steiner, H. Y., & Hunt, M. D.  
617 (1996). Systemic acquired resistance. *Plant Cell*, *8*, 1809–1819.
- 618 Sato, T., Fujikake, H., Ohtake, N., Sueyoshi, K., Takahashi, T., Sato, A., et al. (2002). Effect of  
619 exogenous salicylic acid supply on nodulation formation of hypernodulating mutant and wild  
620 type of soybean. *Soil Science Plant Nutrition*, *48*, 413–420.
- 621 Schenk, P. M., Kazan, K., Rusu, A. G., Manners, J. M., & Maclean, D. J. (2005). The SEN1 gene  
622 of *Arabidopsis* is regulated by signals that link plant defence responses and senescence. *Plant*  
623 *Physiology and Biochemistry*, *43*, 997–1005.
- 624 Shah, J., Kachroo, P., Nandi, A., & Klessig, D. F. (2001). A recessive mutation in the Arabidopsis  
625 SSI2 gene confers SA and NPR1-independent expression of PR genes and resistance against  
626 bacterial and oomycete pathogens. *Plant Journal*, *25*, 563–574.
- 627 Shakirova, F. M. (2007). Role of hormonal system in the manifestation of growth promoting and  
628 anti-stress action of salicylic acid. In S. Hayat & A. Ahmad (Eds.), *A plant hormone*.  
629 Dordrecht: Springer.
- 630 Shao, L., Shu, Z., Sun, S. L., Peng, C. L., Wang, X. J., & Lin, Z. F. (2007). Antioxidation of  
631 anthocyanins in photosynthesis under high temperature stress. *Journal of Integrative Plant*  
632 *Biology*, *49*, 1341–1351.
- 633 Sharafizad, M., Naderi, A., Ata Siadat, S., Sakinejad, T., Lak, S. (2012). Effect of salicylic acid  
634 pretreatment on yield, its components and remobilization of stored material of wheat under  
635 drought Stress. *Journal of Agriculture Science*, **10**: (In press). doi:10.5539/jas.v4n10p115.

- 636 Simpson, G. G., & Dean, C. (2002). Arabidopsis, the Rosetta stone of flowering time? *Science*,  
637 296, 285–289.
- 638 Slaymaker, D. H., Navarre, D. A., Clark, D., Del-Pozo, O., Martin, G. B., & Klessig, D. F. (2002).  
639 The tobacco salicylic acid binding protein 3 (SABP3) is the chloroplast carbonic anhydrase,  
640 which exhibits antioxidant activity and plays a role in the hypersensitive defense response.  
641 *Proceedings of the National Academy of Sciences of the United States of America*, 99,  
642 11640–11645.
- 643 Srivastava, M. K., & Dwivedi, U. N. (2000). Delayed ripening of banana fruit by salicylic acid.  
644 *Plant Science*, 158, 87–96.
- 645 Szalai, G., Tari, I., Janda, T., Pestenác, A., & Páldi, E. (2000). Effects of cold acclimation and  
646 salicylic acid on changes in ACC and MACC contents in maize during chilling. *Biologia*  
647 *Plantarum*, 43, 637–640.
- 648 Todd, J. F., Paliyath, G., & Thompson, J. E. (1990). Characteristics of a membrane-associated  
649 lipooxygenase in tomato fruit. *Plant Physiology*, 94, 1225–1232.
- 650 Uzunova, A. N., & Popova, L. P. (2000). Effect of salicylic acid on leaf anatomy and chloroplast  
651 ultrastructure of barley plants. *Photosynthetica*, 38, 243–250.
- 652 van Spronsen, P. C., Tak, T., Rood, A. M. M., van Brussel, A. A. N., Kijne, J. W., & Boot, K.  
653 J. M. (2003). Salicylic acid inhibits indeterminate-type nodulation but not determinate-type  
654 nodulation. *Molecular Plant Microbe Interactions*, 16, 83–91.
- 655 Verica, J. A., & Medford, J. I. (1997). Modified MER15 expression alters cell expansion in  
656 transgenic Arabidopsis plants. *Plant Science*, 125, 201–210.
- 657 Vlot, C. A., Dempsey, M. A., & Klessig, D. F. (2009). Salicylic acid, a multifaceted hormone to  
658 Combat disease. *Annual Review of Phytopathology*, 2009(47), 177–206.
- 659 Vogelmann, K., Drechsel, G., Bergler, J., Subert, C., Philippar, K., Soll, J., et al. (2012). Early  
660 senescence and cell death in *arabidopsis saull* mutants involves the *pad4*-dependent salicylic  
661 acid pathway. *Plant Physiology*, 159, 1477–1487.
- 662 Wada, K. C., Yamada, M., Shiraya, T., & Takeno, K. (2010). Salicylic acid and the flowering  
663 gene FLOWERING LOCUS T homolog are involved in poor-nutrition stress-induced  
664 flowering of *Pharbitis nil*. *Journal of Plant Physiology*, 167, 447–452.
- 665 Wang, L. J., Fan, L., Loescher, W., Duan, W., Liu, G. J., & Cheng, J. S. (2010). Salicylic acid  
666 alleviates decreases in photosynthesis under heat stress and accelerates recovery in grapevine  
667 leaves. *BMC Plant Biology*, 10, 34–40.
- 668 Wilson, R. N., Heckman, J. W., & Somerville, C. R. (1992). Gibberellin is required for flowering  
669 in Arabidopsis thaliana under short days. *Plant Physiology*, 100, 403–408.
- 670 Xie, Z., Zhang, Z. L., Hanzlik, S., Cook, E., & Shen, Q. J. (2007). Salicylic acid inhibits  
671 gibberellin-induced alpha-amylase expression and seed germination via a pathway involving  
672 an abscisic-acid inducible WRKY gene. *Plant Molecular Biology*, 64, 293–303.
- 673 Xu, W. P., Chen, K. S., Li, F., & Zhang, S. L. (2000). The regulations of lipooxygenase, jasmonic  
674 acid, and salicylic acid on ethylene biosynthesis in ripening *Actinidia* Fruits. *Acta*  
675 *Phytolphysiol. Sin.*, 26, 507–514.
- 676 Yıldırım, E., & Dursun, A. (2009). Effect of foliar salicylic acid applications on plant growth and  
677 yield of tomato under greenhouse conditions. *Acta Horticulture*, 807, 395–400.
- 678 Yokoyama, R., & Nishitani, K. (2001). A comprehensive expression analysis of all members of a  
679 gene family encoding cell-wall enzymes allowed us to predict cis-regulatory regions involved  
680 in cell-wall construction in specific organs of Arabidopsis. *Plant and Cell Physiology*, 42,  
681 1025–1033.
- 682 Yusuf, M., Hasan, S. A., Ali, B., Hayat, S., Fariduddin, Q., & Ahmad, A. (2008). Effect of  
683 salicylic acid on salinity induced changes in *Brassica juncea*. *Journal of Integrative Plant*  
684 *Biology*, 50, 1–4.
- 685 Yusuf, M., Fariduddin, Q., Varshney, P., & Ahmad, A. (2012). Salicylic acid minimizes nickel  
686 and/or salinity-induced toxicity in Indian mustard (*Brassica juncea*) through an improved  
687 antioxidant system. *Environmental Science and Pollution Research*, 19, 8–18.

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