

MANAGING PLANT STRESS USING SALICYLIC ACID: PHYSIOLOGICAL AND MOLECULAR ASPECTS

EDITED BY

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Managing Plant Stress Using Salicylic Acid

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Physiological and Molecular Aspects

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Preface

Plants, during their life, encounter various challenges, and one of the main threats for their normal development is abiotic stress. The major abiotic stresses possessing threat to plants are water scarcity, salinity, extreme temperatures, heavy metals, and pesticides. All these abiotic factors can cause phytotoxicity, either directly or indirectly, resulting in interruption to plant's growth and development which eventually decrease plant yield. Researchers all over the world have already specified abiotic stresses as the main danger for agrarian systems. However, plant's internal defense system tries to counterattack the negative impacts of abiotic stresses by regulating their biological processes. But, above a threshold level of a particular stress, even plant's internal antioxidative defense system is unable to entirely protect plants from the deleterious effects of abiotic stress. So, plants need some external stimulus or support to boost the level of defense system to survive under challenging environments. Exogenous application of plant hormones is one of the best and eco-friendly approaches to trigger the defense system of stressed plants.

In the recent past, a lot of investigations have been focused on studying the mechanisms of plant hormone-mediated regulation of plant growth and development under abiotic stress conditions. Salicylic acid is an important plant hormone which acts a multifunctional molecule and regulates key physiological and biochemical processes in plants. This hormone also provides resistance to plants against abiotic stresses by regulating key cell signaling pathways. Exogenous application of SA helps in convalescing the growth and development of stressed plants by reducing the oxidative stress accompanied by enhanced performance of antioxidative defense machinery. At present, scientists all over the world are very keen to study the deep mechanisms of SA-modulated abiotic stress responses by using various advanced molecular techniques. These advancements in research approach can be beneficial in exploring some important genetic pathways which can be applied to develop abiotic stress-tolerant plant varieties. So, recently, many studies have been carried out to find the deep molecular mechanisms explaining SA-mediated regulation of plant growth under abiotic stress. So, our purpose is to compile all the latest developments described in the arena of SA-mediated regulation of abiotic stress.

The first chapter explains the general roles of salicylic acid in plant biology. Chapter 2 discusses the role of salicylic acid in plants during stressful conditions in relation to omics approaches. Chapter 3 focuses on describing the possible role of salicylic acid in regulation of primary metabolisms like respiration and photosynthesis in plants growing under challenging conditions. The next chapter discusses salicylic acid-mediated secondary metabolism

in plants under abiotic stress. Further chapters explore the role of salicylic acid in stressed plants by important aspects like mineral nutrition, seed germination to fruit maturation. Chapter 7 brings the updated knowledge about the role of salicylic acid in the postharvest technology. The next chapters focus on exploring salicylic acid-mediated physiological and molecular mechanism in plants under stresses like metal(loid), heat, chilling, and drought. Chapter 14 describes in detail the regulation of photosynthesis by salicylic acid under optimal and suboptimal conditions. Further chapters focus on describing the roles of salicylic acid in mediating stress conditions in plants at genetic levels including the phytohormonal cross talk and post-transnational modifications.

This book is a collection of recent developments in the field of salicylic acid biology in relation to challenging environment conditions. To the academic and industry sectors, the book provides useful hints for the development of eco-friendly stress-mediating approaches as well as helps to understand the future importance and involvement of salicylic acid in safe food production. Therefore, we believe that this book will be a vital source of information for scientists and academics working in the field of abiotic stress tolerance.

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1

Salicylic Acid: A Regulator of Plant Growth and Development

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Introduction

In plants, the phytohormones act as endogenous signals, both spatially and temporally, regulating a number of physiological functions. The cross talk between various phytohormones helps the plant to withstand biotic and abiotic stresses. This cross talk of plant hormones has evolved into a complex network within the plants, thus helping the plants having a balanced reaction to developmental and environmental stimuli (Sharma et al. 2018, 2019a; Koo et al. 2020). Salicylic acid (SA) or ortho-hydroxybenzoic acid is a member of the group of plant phenolics with a seven-carbon (C) skeleton. A study of reproductive structures and leaves of 34 plant species confirmed that SA is ubiquitously distributed in plant kingdom (Raskin et al. 1990). The name SA is from *Salix* (Latin word) as it was found to be an active constituent of willow tree bark (*Salix* sp.) which was used extensively to cure fever and aches (Khan et al. 2015).

The biosynthesis of SA in plants involves the isochorismate synthase (ICS) pathway and phenylalanine ammonia-lyase (PAL) pathway (Janda et al. 2014). The ICS pathway was first discovered in *Pseudomonas* species and the *PmsCEAB* gene cluster was found to play the key role in the synthesis of SA. The conversion of chorismate to isochorismate (IC) is catalyzed by *PmsC* gene and then isochorismate pyruvatelyase encoded by the *PmsB* gene converts IC to SA making SA synthesis from chorismate a two-step process (Mercado-Blanco et al. 2001; Lefevere et al. 2020). In the PAL pathway, the key enzyme is chorismate mutase (CM) which catalyzes the process of converting CM to prephenate. Prephenate gets converted to phenylalanine (Phe), which in turn is converted to trans-cinnamic acid (tCA) by the enzyme PAL. The next step involves the catalyzing of the conversion of tCA to benzoic acid (BA) by abnormal inflorescence meristem1 (AIM1), which is a multifunctional protein (MFP) family member (Rylott et al. 2006; Arent et al. 2010). The last step in the PAL

pathway is the conversion of BA to SA which is presumed to be catalyzed by benzoic acid hydroxylase (Lefevere et al. 2020).

The ICS as well as PAL pathways to synthesize SA start from chorismate, and the importance of both ICS and PAL varies in different species of plants, as not all enzymes which catalyze various reactions in these pathways have been found in all plants. The ICS pathway plays an important role in SA biosynthesis in *Arabidopsis*, and PAL has been found to be more important in rice, while in soybeans, both pathways contribute equally (Silverman et al. 1995; Duan et al. 2014).

In plants, SA plays a significant part in the growth, development, and in the protection from biotic and abiotic stresses (Khan et al. 2015; Sharma et al. 2019b, 2020; Prakash et al. 2021) (Figure 1.1). The role of SA in defense mechanisms of plant was established during the last 30 years and before that it was recognized as an unimportant secondary plant metabolite. Since 1979, when White (1979) reported the role of SA in tobacco plants' disease resistance, numerous findings showed the role of SA as an important regulatory substance in plants (Chen et al. 2009). Studies have shown that in plants, SA plays a vital part in disease resistance, DNA damage/repair, seed germination, fruit yield, and thermogenesis (Dempsey and Klessig 2017). Increased levels of SA are seen in the presence of an infection, and if supplied exogenously, SA strengthens the plant defense system (Lefevere et al. 2020). In this review, we have focused on the role of SA in plants as a regulator of growth and development and providing resistance against various stresses.

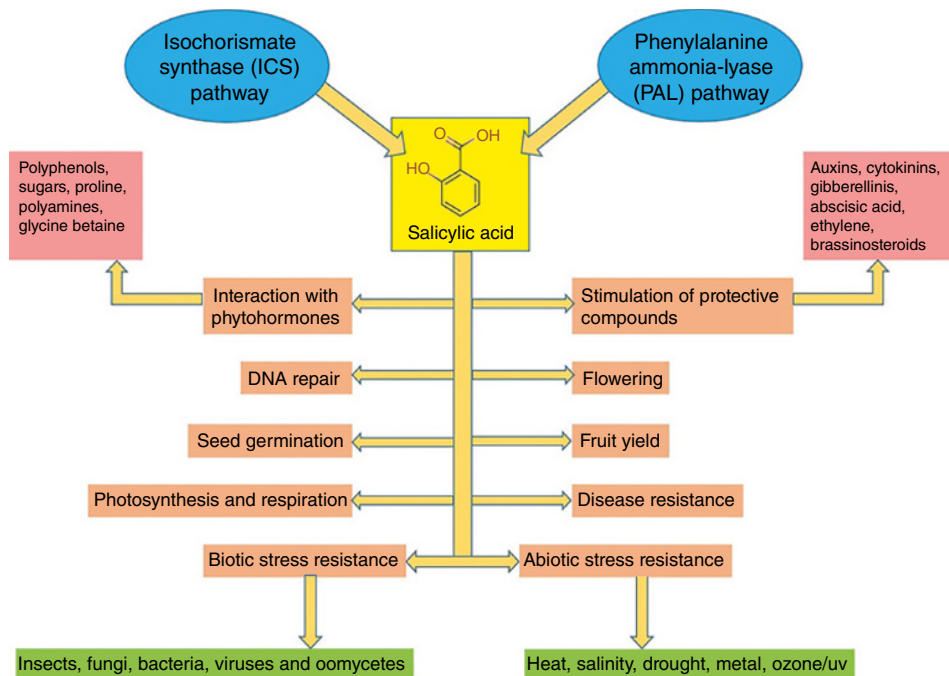


Figure 1.1 Schematization of the role of salicylic acid in plants. *Source:* Based on Khan et al. 2015; Sharma et al. 2019b, Sharma et al. 2020; Prakash et al. 2021.

Salicylic Acid and Plant Growth

SA plays an important role in plant growth, along with other phytohormones, and its effects on growth, when applied exogenously, is affected by the species of the plant and its stage of development as well as its concentration (Vicente and Plasencia 2011). It has been reported that more than 1 mM of SA is considered a high concentration and has negative effects (Koo et al. 2020). Barley and maize seeds did not show any germination when imbibed in >3 mM of SA (Guan and Scandalios 1995; Xie et al. 2007). On the contrary, when maize seeds were imbibed in ~ 0.3 mM– ~ 0.9 mM of SA, an increased germination speed and enhanced shoot length were recorded (Sallam and Ibrahim 2015). SA (aqueous solution), when applied to soybean shoots in the form of spray, increased the shoot and root growth significantly. Although, photosynthetic rate was not found to have any significant effect with this treatment (Gutiérrez-Coronado et al. 1998). In soybean, wheat, maize, and chamomile, SA has been found to stimulate growth. An increased growth of ~ 20 and 45% in the shoots and roots, respectively, was observed in soybean plants when treated with 10 nM, 100 μ M, and up to 10 mM of SA. In wheat seedlings, development of larger ears and enhancement of cell division was observed in the shoot apical meristems, with a treatment of 50 μ M SA. In chamomile plants, 50 μ M SA stimulated the growth and an opposite effect was observed at a concentration of 250 μ M SA (Gutiérrez-Coronado et al. 1998; Shakirova et al. 2003; Gunes et al. 2007; Kováčik et al. 2009). In apple, strawberry, and mango plants, fruit setting was enhanced with SA treatment (Shaaban et al. 2011; Kazemi 2013; Ngullie et al. 2014).

The relationship between SA, reactive oxygen species (ROS), and mitogen-activated protein kinase (MAPK) cascades has been found to be very important in regulating plant growth. Zhang and Klessig (1997) found that *Arabidopsis* MPK6 is an orthologue of tobacco SA-induced protein kinase (SIPK), and has been suggested to have an important role in growth and development (Bush and Krysan 2007; Wang et al. 2007, 2008). It has been reported that in regulation of cell growth, MAPK cascades act as mediators between phytohormones, SA, and ROS signaling (Foreman et al. 2003; Potocký et al. 2007).

SA also plays an important role in regulating flowering. Lee and Skoog (1965) indicated its flower-inducing effects for the first time. 4 μ M SA was reported to promote flower bud formation from callus of tobacco. Then, Cleland and Ajami (1974) reported the isolation and identification of SA in aphid honeydew as the substantial factor for flower induction in short-day plant *Xanthium strumarum*. Later, SA's role in *Impatiens balsamina*, *Oncidium* (orchid species), *Pisita stratiotes* L., and *Arabidopsis thaliana* as a stimulatory factor on flowering was demonstrated. In thermogenic plants, the inflorescences were found to have high levels of endogenous SA (Raskin et al. 1990), while in non-thermogenic plants, SA levels were found to increase twofold in tobacco and fivefold in *Arabidopsis* leaves at the time of initiation or transition toward flowering (Yalpani et al. 1993; Abreu and Munné-Bosch 2009). Similarly, *Arabidopsis* plants, which were SA deficient (NahG, sid1/eds5, and sid2) exhibited a phenotype having late flowering (Martínez et al. 2004). In sunflower, it was discovered that the transcription factor HAHB10 (belonging to HD-Zip II family) plays a role in responding to biotic stress and inducing flowering and it was observed that treatment with SA induces the HAHB10 expression (Dezar et al. 2011).

However, the possibility of endogenous regulation by SA alone in case of flowering was weakened as there was not much difference in the levels of SA in aphid honeydew from

flowering as well as vegetative plant parts. Thus, it was established that SA promotes and regulates flowering in conjugation with other plant growth regulators (Raskin 1992).

Salicylic Acid and Photosynthesis

In plants, photosynthesis is considered to be a very delicate physiological process. Heat stress can harm the photosynthetic apparatus, and plants have developed protective mechanisms like dissipating the excess excitation energy, utilizing heat shock proteins and plant growth regulators. SA has been reported to play a significant part during abiotic stresses to plants (Wang et al. 2010; Kohli et al. 2017, 2018). SA application enhanced the photosynthetic capacity in barley and spring wheat plants which were exposed to salt and drought stress (El-Tayeb 2005; Arfan et al. 2007). In tobacco and Arabidopsis, when SA was applied exogenously, it improved the heat tolerance (Dat et al. 1998a, 1998b; Lopez-Delgado et al. 1998; Senaratna et al. 2003; Clarke et al. 2004). In heat-stressed young grape leaves, the thiobarbituric acid reactive substances were decreased upon spraying with SA (0.1 mM solution) which indicates that SA helped in tolerance of intrinsic heat stress (Wang and Li 2006).

In a study conducted by Fariduddin et al. (2003), foliar application of SA (aqueous solution) to 60 days old *Brassica juncea* plants showed higher net photosynthetic rate and increased pod count and seed yield as compared with the control. Studies have suggested that SA plays a significant role in photosynthesis as it affects the structure of chloroplast and leaf (Uzunova and Popova 2000), contents of carotenoid and chlorophyll, and closure of stomata. It has also been reported to affect the carbonic anhydrase as well as RuBisCO (ribulose-1,5-bisphosphate carboxylase/oxygenase) enzymes (Vicente and Plasencia 2011). Haroun et al. (1998) reported that SA application promotes photosynthetic pigments in the leaves of lupine (*Lupinus termis* Forssk.). Further, a study conducted on Egyptian Lupine confirmed that foliar application of SA (25, 50, and 75 ppm) resulted in a rise in chlorophyll a, b and carotenoids in leaves (Gomaa et al. 2015).

The closing of stomata in plants is controlled by different phytohormones, and is considered to undertake a vital role in photosynthesis (Acharya and Assmann 2009). Studies have shown a significant role of SA in the functioning of guard cells, which is in turn essential for the closure of stomata (Melotto et al. 2006). Mateo et al. (2004) reported that stomatal gas exchange was reduced fourfold within two hours after treating *Arabidopsis* with 0.4 mM SA.

Salicylic Acid and Respiration

SA plays a significant role in regulating the alternative oxidase pathway (AOX) via induction of its gene expression (Kapulnik et al. 1992; Rhoads and McIntosh 1992). AOX, for maintaining the growth rate homeostasis, leads a controlled synthesis of ATP as non-proton-driven carrier (Moore et al. 2002). AOX is further reported to decrease the production of ROS in mitochondria. Thus, SA targeting AOX plays a significant role for regulation of plant growth. Studies have also emphasized on the role of SA in controlling the oxidative phosphorylation and electron transport in plant mitochondria (Xie and Chen 1999; Norman et al. 2004).

Adding 2–20 μM SA in a cell suspension culture of tobacco resulted in increased cyanide-resistant O_2 uptake. Calorimetric measurements showed an increase of 60% in the rate of evolution of heat from the cells (Kapulnik et al. 1992). SA has been reported to exert a dual action on mitochondrial respiration, depending on concentration, in plant and animal mitochondria. At a lower concentration (0.1–1.0 mM), on the oxidative phosphorylation, it exerts mainly an uncoupling reaction, helping in increasing the substrate oxidation rate. At a high concentration (more than 1 mM), SA significantly suppressed State 3 respiration (Howell et al. 2004; Nulton-Persson et al. 2004; de Souza et al. 2011). In a study conducted in the mitochondria of sugarbeet (*Beta vulgaris* L.), taproots, and lupine (*Lupinus luteus* L.) cotyledons, to understand the effect of SA on generation of membrane potential ($\Delta\psi$) at malate oxidation, it was observed that the $\Delta\psi$ dissipation was a result of the uncoupling and inhibitory action of SA on respiration. It was concluded that in a plant cell under stress, increased concentration of SA has a direct and strong effect on the basic mitochondrial functions, viz., ATP synthesis, oxidation of respiratory substrates, ROS production, and membrane potential generation and the degree of the extent of these effects not only depends on the amount of time the organelle was exposed to SA but also on its concentration and the mitochondrial structure and function in different plants and animals (Shugaev et al. 2014).

Salicylic Acid and Abiotic and Biotic Stress

Agricultural productivity all over the world is affected by abiotic and biotic stresses to the plants (Handa et al. 2018, 2019; Wang et al. 2019; Arif et al. 2019; Roychoudhury and Tripathi 2019; Kapoor et al. 2019, 2020; Deshmukh et al. 2020; Roychoudhury and Tripathi 2020; Dhiman et al. 2021). Plant growth regulators are well known to be involved in the plant-responses to stress (Yadav et al. 2018; Singh et al. 2020). SA has been found to induce stress resistance in plants having biotic stress (Kumar 2014) and also to increase tolerance to abiotic stresses such as heat, salinity, drought, and metal (Khan and Khan 2013; Fayeze and Bazaid 2014; Khan et al. 2014; Zhang et al. 2015; Prakash et al. 2021). An application of SA exogenously to *Oryza sativa*, *Zea mays*, and *Phaseolus vulgaris* plants exposed to lead, cadmium, and copper metal stresses were found to have improved photosynthetic traits as well as enhanced growth. It also modulated the antioxidant defense system of the plants (Krantev et al. 2008; Zengin 2014; Arif et al. 2016). The exogenous application of SA increased endogenous SA content by enhancing *OsWRKY45* gene expression, which in turn lowered the H_2O_2 content and thus prevented membrane damage in *Oryza sativa* plants exposed to cadmium metal stress (Chao et al. 2010). Similarly, Belkadhri et al. (2015) also reported that SA regulated the H_2O_2 accumulation and thus resulted in an enhanced tolerance to Cd in *Linum usitatissimum*. Chlorosis caused by Fe deficiency has also been reported to be inhibited by SA (Kong et al. 2014).

In crops like *Vicia faba*, *Brassica juncea*, *Medicago sativa*, and *Vicia radiata*, SA has been found to strengthen the stress mechanism against salinity stress (Azooz 2009; Nazar et al. 2011, 2015; Palma et al. 2013; Khan et al. 2014). In case of *Triticum aestivum*, exogenous application of SA (0.5 mM) resulted in an improvement of salt stress tolerance via increase in the enzyme activity of ascorbate-GSH pathway and enhancement in the level of GPX1,

GPX2, DHAR, GR, GST1, GST2, MDHAR, and GS antioxidant genes (Li et al. 2013). Similarly, in case of Ozone stress to plants, SA promotes molecular and physiological changes as it works as a signal molecule (Tamaoki 2008). It has also been suggested that SA plays a role in the signaling network which integrates phytohormones like JA, ethylene in ozone-stressed plants (Rao et al. 2002). The modulation of antioxidative enzymes, detoxification of superoxide radicals, prevention of oxidative damage, and protection of metabolic enzymes and membranes have been reported following exogenous SA application in plants which are UV-B radiation stressed (Mohammed and Tarpley 2009). A decrease in chromosome aberration level caused by UV-B in the meristematic root tip cells of *Crepis capillaris* was reported with the application of SA (Rančelienė and Vyšniauskienė 2012). Li et al. (2014) reported significant improvement in photosynthetic function, when SA was applied exogenously to plants exposed to UV-B.

There are studies on the significant part of SA in plants having temperature stress. Modulation of antioxidant enzymes in temperature-stressed (2°C) *Z. mays* has been reported by Janda et al. (1999). Under chilling stress, SA was found to protect ultrastructures in the seedlings of *Musa acuminata* (Kang et al. 2007). In *Hordeum vulgare* genotypes, exogenous application of SA enhanced antioxidant enzyme and ice nucleation activity and thus provided cold tolerance (Mutlu et al. 2013). Similarly, in lemon fruit, SA increased total phenolics synthesis and also improved tolerance to chilling temperature (Siboza et al. 2014). In case of drought stress, a number of studies have reported the stress mitigation role of SA application. Habibi (2012) reported an increase in the rate of net CO₂ assimilation and plant dry mass when supplemented with 500 μM SA to drought-stressed *H. vulgare* plants. A foliar application (1.0 μM of SA) was found to enhance the antioxidative defense system in *Z. mays* plants (draught-tolerant vs. drought-sensitive cultivar) exposed to drought stress (Saruhan et al. 2012). It has been reported that oHCA was associated with the biosynthesis of SA and thus played an important part in providing drought tolerance to *O. sativa* plants (Pál et al. 2014).

SA has also been found as a key element in providing the plants the resistance to various microbial pathogens like fungi, bacteria, viruses, and oomycetes (Kunkel and Brooks 2002; Vlot et al. 2009). Glazebrook (2005) established a positive correlation between resistance responses of plants against hemibiotrophic and biotrophic pathogens and the levels of endogenous SA. In case of *Citrus sinensis* plants, a 45% reduction in disease caused by *Xanthomonas axonopodis* was reported (Wang and Liu 2012). The resistance of tomato and Arabidopsis plants was enhanced against *Botrytis cinerea* with the application of SA (Ferrari et al. 2003; Li and Zou 2017). Similarly, treating tomato plants with SA has also been reported to provide resistance against *Fusarium oxysporum* and *Alternaria alternata* (Esmailzadeh et al. 2008; Jendoubi et al. 2015). A retarded nymph development was observed in case of *Oebalus pugnax*, which is a piercing and sucking insect, when SA was applied exogenously to *O. sativa* plants (Stella de Freitas et al. 2019).

The exogenous treatment of plants subjected to pathogen stress with SA results in enhanced expression of pathogenesis-related genes (*PR1*, *PR2*, and *PR5*) and this overexpression of genes increases tolerance to not only pathogens but also various other abiotic stresses (Hong and Hwang 2005; Sarowar et al. 2005; Ali et al. 2018). The mechanism of SA-induced tolerance to plants against stress can include various steps like osmolyte accumulation (glycinebetaine, proline, soluble sugars, and amines), thus maintaining osmotic homeostasis, enhancing

scavenging of ROS, production of stress proteins, regulation of transpiration, mineral uptake regulation, inhibition of ethylene synthesis, and increase in the production of secondary plant metabolites (Horváth et al. 2007; Khan et al. 2015; Emamverdian et al. 2020).

Conclusions

Plants' growth and regulation requires a regular cross talk between various plant growth regulators, among which SA has been found to play a vital role. Seed germination, plant physiological functions, flowering, and tolerance against abiotic and biotic stresses are the various aspects of plant growth and regulation, where the role of SA has been found and elaborated in various research studies. Since its discovery as a healing substance obtained from the bark of willow tree, SA has been proved to be valuable not only for humans but also for plants. There are certain reports which suggest that application of SA over a certain amount brings negative effects. Thus, studies involving exogenous application of SA in an optimal amount for positive plant growth and negative growth of unwanted plants in crop production can open new aspects. Further, manipulating levels of endogenous SA in transgenic plants can open new areas in crop biotechnology and thus help in growing crops with positive growth and increased stress tolerance.

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