# Role of Salicylic Acid in Survival Strategy of Plants under Changing Environment

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## Publication Info

**Abstract**

In recent years salicylic acid (SA) has been the focus of intensive research due to its function as an endogenous signal mediating role in defense responses after pathogen attack. SA antagonizes gene induction by the stress signaling molecule jasmonic acid (JA). It has also been found that SA plays a role during the plant responses to abiotic stresses. The discovery of its targets and understanding of its mechanism of the action in physiological and molecular processes could help in the sustainable plant productivity. Present report focused on various survival strategies of plants under changing environment and the role of SA in cross-talk signaling, osmoregulation, anti-oxidative system and induction of protein kinases under adverse environmental conditions.

## 1. Introduction

Plants require energy (light), water, carbon and mineral nutrients for their growth and development. The natural environment for plants is composed of a complex set of abiotic and biotic stresses which limits crop production world wide. Rarely, is there a single abiotic stress affecting a plant; almost always there are interacting factors responsible for changes in the plant metabolism. Plants have acquired specific mechanisms to combat with these stresses (Ramegowda and Senthil-Kumar, 2015). Abiotic stresses are defined as environmental conditions (drought, salinity, high temperature, cold and chemical compounds) that reduce growth, yield and even survival of the plants (Cramer, 2010; Pandey and Chikara, 2014; Singh *et al*., 2015). Plant responses to these stresses are dynamic and complex. These are both elastic (reversible) and plastic (irreversible) (Cramer *et al*., 2011). One of the earliest metabolic responses to abiotic stresses and the inhibition of growth is the inhibition of protein synthesis and an increase in protein folding and processing. Energy metabolism is affected as the stress becomes more severe (e.g. sugars, lipids and photosynthesis). Thus, there are gradual and complex changes in metabolism in response to stress. One of the earliest signals involved in many abiotic stresses are reactive oxygen species (ROS) and reactive nitrogen species (RNS), which modify enzyme activity and gene regulation. ROS and RNS form a coordinated network that regulates many plant responses to the environment; there are a large number of studies on the oxidative effects of ROS on plant responses to abiotic stress (Apel and Hirt, 2004; Osakabe *et al*., 2013).

Plant hormones play important roles in regulation of developmental processes and signaling networks in plants under abiotic stresses. Recent researches have shown potential of phytohormones in reducing or eradicating the negative effects of abiotic stress. In the list of known classical plant hormones, salicylic acid (SA) and jasmonic acid (JA) have been recently added and have shown as potential tool in enhancing tolerance of plants to abiotic stress. SA participates in the regulation of physiological and molecular mechanisms to adjust plants in adverse environmental conditions. SA has been recognized as a regulatory signal mediating plant response to abiotic stresses such as drought (Munne-Bosch and Penelas, 2003), chilling (Kang and Saltveit, 2002) heavy metals and osmotic stress (Metwally *et al*., 2003). However, most of the research on this hormone has focused on its role in the local and systemic response against microbial pathogens, and on defining the transduction pathway leading to gene expression induced by SA. SA also regulates processes such as seed germination, vegetative growth, photosynthesis, respiration, thermogenesis, flower formation, seed production, senescence, and a type of cell death that is not associated with the hypersensitive response. In addition, SA could contribute to maintaining cellular redox homeostasis through the regulation of antioxidant enzymes activity and

regulation of gene expression by inducing an RNA dependent RNA polymerase that is important for post-transcriptional gene silencing (Durner and Klessig, 1995; Caarls *et al.*, 2015). This article briefly coveres the recent work on SA signaling and its role in growth and development of plants under adverse environmental conditions.

## 2. Plant Responses to Adverse Environmental Conditions

Plants have evolved adaptive mechanisms that allow them to survive in an ever-changing environment. External stimuli activate the receptor molecules and initiate complex downstream signaling networks that exhibit cross-talk in order to respond to various environmental and developmental cues in an appropriate and integrated manner. These stresses often result in significant decreases in the yield of native plants and economically important crop plants. Due to the negative impact on growth and yield, the plant developed mechanistic in stress response and adaptation, such as stress signaling and the regulation of gene expression to improving stress tolerance in plants (Singh *et al.*, 2011; Osakabe *et al.*, 2013).

Although the interaction between biotic and abiotic factors in plants was analyzed in the past several years through extrapolation of information from individual stress responses, yet, the physiological and molecular responses that occur in plants exposed to a combination of simultaneous biotic and abiotic stresses remain elusive. The available evidences indicate that simultaneous occurrence of biotic and abiotic stresses can cause either a negative (i.e. susceptibility) or positive (i.e., tolerance) effects on plants depending on the stress and pathogen under study (Singh *et al.*, 2011). Reports on combined pathogen and high temperature stress indicate that high temperature increases the disease susceptibility of plants. In tobacco (*Nicotiana tabacum*) and pepper (*Capsicum annuum*), high temperature suppressed its resistance to Tobacco mosaic virus (TMV) and Tomato spotted wilt virus (TSWV), respectively. In *Arabidopsis* and *N. benthamiana*, both basal and the resistance gene-mediated defense responses against *Pseudomonas syringae* were inhibited under high temperature. Hypersensitive response (HR) induced by R-genes against Potato virus X (PVX) and TMV was also delayed in plants exposed to high temperature stress. These studies indicate that both basal and the R-gene-mediated defense responses are suppressed during combined high temperature and pathogen infection, and this trend is not seen in plants exposed to individual stresses. Contrast to the above mentioned studies on increased susceptibility, several other studies documented resistance responses of plants during combined biotic and abiotic stresses. Occurrence of high temperature stress in combination with *Puccinia striiformis* (causal agent of stripe rust) infection enhanced disease resistance in *Triticum aestivum*. Salinity stress also increased resistance of barley (*Hordeum vulgare*) plants to *Blumeria graminis* (causal agent of powdery mildew) in a concentration dependent manner. Salinity stress can exert both osmotic and ion toxicity effects potentially restricting the pathogen growth. Exposure of rice plants to combined drought stress and plant-parasitic nematode infection ameliorated the severity of drought stress (Atkinson and Urwin, 2012). Taken together, these studies indicate that during simultaneous biotic and abiotic stresses, plants exhibit a complex and differential response leading to resistance or susceptibility of plants.

## 3. Salicylic Acid Induced Mitigation in Plants

SA or ortho-hydroxy benzoic acid and other salicylates are known to affect various physiological and biochemical activities of plants and may play a key role in regulating their growth and productivity under adverse environmental conditions. SA has a wide range of distribution in plants and has variable concentrations among species, with up to 100-fold differences have been recorded (Raskin *et al.*, 1990). SA is synthesized through two distinct and compartmentalized pathways that employ different precursors: The phenylpropanoid route in the cytoplasm initiates from phenylalanine, and the isochorismate pathway occurs in the chloroplast. Most of the SA synthesized in plants are glucosylated and/or methylated. Glucose conjugation at the hydroxyl group of SA results in formation of the SA glucoside (SA 2-O-$\beta$-D-glucoside) as a major conjugate, whereas glucose conjugation at the SA carboxyl group produces the SA glucose ester in minor amounts. These conjugation reactions are catalysed by cytosolic SA glucosyltransferases that are induced by SA application or pathogen attack in tobacco and *Arabidopsis* plants (Lee and Raskin, 1999; Song, 2006). Interestingly, SA is also converted to methyl salicylate (MeSA) by an SA carboxyl methyltransferase, and this volatile derivate is an important long-distance signal in tobacco and *Arabidopsis* systemic acquired resistance (Shulaev *et al.*, 1997; Park *et al.*, 2007; Vlot *et al.*, 2008). A major goal of phytohormonal ecology is to understand the role of plant hormones in determining plant responses to various environmental challenges. This includes the strategy that each hormone plays in response to

individual stress as well as the coordination of multiple hormones in response to multiple stresses (Singh *et al.*, 2011). SA is a phenolic growth regulator, which takes transcription control over phytohormonal signaling and participates in the regulation of physiological and molecular mechanisms to adjust plants in adverse environmental conditions (Caarls *et al.*, 2015).

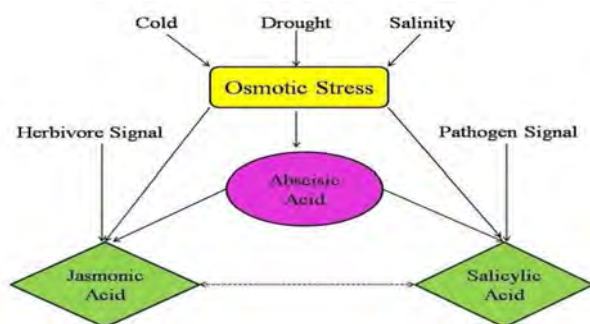### 3.1. Salicylic acid and stress signailing

SA is reported as a potent signaling molecule in plants and involved in eliciting specific responses to biotic and abiotic stresses. The role of SA as a defense signal has been well established and has been suggested as signal transducer or messenger under stress conditions (Lopez *et al.*, 2008). It was shown that exogenous treatment of young maize plants with SA grown under optimal growth conditions provided protection against subsequent low-temperature stress. Treatment of bean and tomato plants with SA or aspirin increased their tolerance against heat, chilling and drought stress (Senaratna *et al.*, 2000). These observations suggest that the role of SA in chilling tolerance is related with its influence on the anti-oxidative enzyme activities and hydrogen peroxide metabolism. Kang and Saltveit (2002) reported that SA-induced chilling tolerance in maize and cucumber plants might be associated with an increase in the activity of glutathione reductase (GR) and peroxidase (POX). More recently Wang and Li (2006) showed that SA treatment of grape plants exposed to low temperature stress led to a decrease in the rates of lipid peroxidation and electrolyte leakage and induced cold tolerance. A certain level of cold tolerance was shown to be induced by SA in winter wheat exposed to low temperature stress. It was suggested that SA could increase the freezing tolerance of winter wheat by affecting apoplastic protein synthesis (Tasgin *et al.*,



**Fig. 1:** Proposed model to show a relationship among abscisic acid-jasmonic acid-salicylic acid signaling pathways in plants in response to biotic and abiotic stresses

2003). Borsani *et al.* (2001) showed an evidence for a role of SA in the oxidative damage generated by NaCl and osmotic stress in *Arabidopsis* seedlings Beside SA, ortho-hydroxy benzoic acid and other salicylates are known to affect various physiological and biochemical activities of plants and may play a key role in regulating their growth and productivity as shown in Fig. 1 (Hayat *et al.*, 2010).

It is reported that the radiolabeled SA was translocated at an unexpectedly rapid rate when applied exogenously at cut end of petiole in tobacco plants (Ohashi *et al.*, 2004). The results of the experiment revealed that the signal reached to 6 neighboring upper leaves and three adjacent lower leaves within a span of 10 min and accumulated throughout the plant body within 50 min, indicating that the transport of SA is rapid and smooth enough to allow a systemic distribution of its signal throughout the plat body within a short span of time, thereby providing tolerance to infections (Ohashi *et al.*, 2004). However, it was further reported that SA can pass through the tough cuticular layer in its methylated form which makes it capable of diffusing across cuticle independent of pH. Methyl salicylate (MeSA) is a volatile long distance signaling molecule that moves from infected to the non-infected tissues through phloem. MeSA represents an inactive precursor of SA that can be translocated and converted to SA whenever required (Hayat *et al.*, 2010). Transcriptional and post-translational regulatory mechanisms are also important in SA controlled signaling pathways (Caarls *et al.*, 2015).

### 3.2. Salicylic acid and osmoregulation

Osmotic response is a common response to many stresses (e.g. water deficit, salinity, high and low temperatures, herbivory, and pathogens) (Tester and Bacic, 2005; Lopez *et al.*, 2008). Either the whole plant experiences osmotic stress or specific cells under 'attack' experience the osmotic stress. The osmotic stress is caused by water loss, which is a general problem for photosynthesizing and transpiring land plants. Salinity is one of the major that causes osmotic stress in plants and ultimately reduction in plant productivity (Borsani *et al.*, 2001). Salinity stress involves changes in various physiological and metabolic processes, depending on severity and duration of the stress, and ultimately inhibits crop production (Gupta and Huang, 2014). During the initial phases of salinity stress, water absorption capacity of root systems decreases and water loss from leaves is accelerated due to osmotic stress of high salt accumulation in soil and plants, and therefore salinity stress is also considered as

hyperosmotic stress (Munns, 2005). Osmotic stress in the initial stage of salinity stress causes various physiological changes, such as interruption of membranes, nutrient imbalance, impairs the ability to detoxify ROS, differences in the antioxidant enzymes and decreased photosynthetic activity, and decrease in stomatal aperture (Munns and Tester, 2008; Rahnama *et al.*, 2010 ). One of the most detrimental effects of salinity stress is the accumulation of $Na^+$ and $Cl^-$ ions in tissues of plants exposed to soils with high NaCl concentrations. Entry of both $Na^+$ and $Cl^-$ into the cells causes severe ion imbalance and excess uptake might cause significant physiological disorder(s). High $Na^+$ concentration inhibits uptake of $K^+$ ions which is an essential element for growth and development that results into lower productivity and may even lead to death. In response to salinity stress, the production of ROS such as singlet oxygen, superoxide, hydroxyl radical, and hydrogen peroxide is enhanced which lead

to oxidative damages in various cellular components such as proteins, lipids, and DNA, interrupting vital cellular functions of plants (Apel and Hirt, 2004; Mahajan and Tuteja, 2005; Ahmad and Prasad, 2012).

### 3.3. Salicylic acid and antioxidant system

The antioxidant defense system in the plant cell constitutes both enzymatic and non-enzymatic components. Enzymatic components include superoxide dismutase (SOD), catalase, POX, ascorbate peroxidase (APX) and GR. Non-enzymatic components contain cysteine, reduced glutathione and ascorbic acid (Gong *et al.*, 2005). The ROS in plants are removed by a variety of antioxidant enzymes and/or lipid-soluble and water soluble scavenging molecules (Hasegawa *et al.*, 2000); the antioxidant enzymes being the most efficient mechanisms against oxidative stress (Durner and Klessing, 1995). Apart from catalase, various POXs and peroxiredoxins, are involved in the ascorbate-
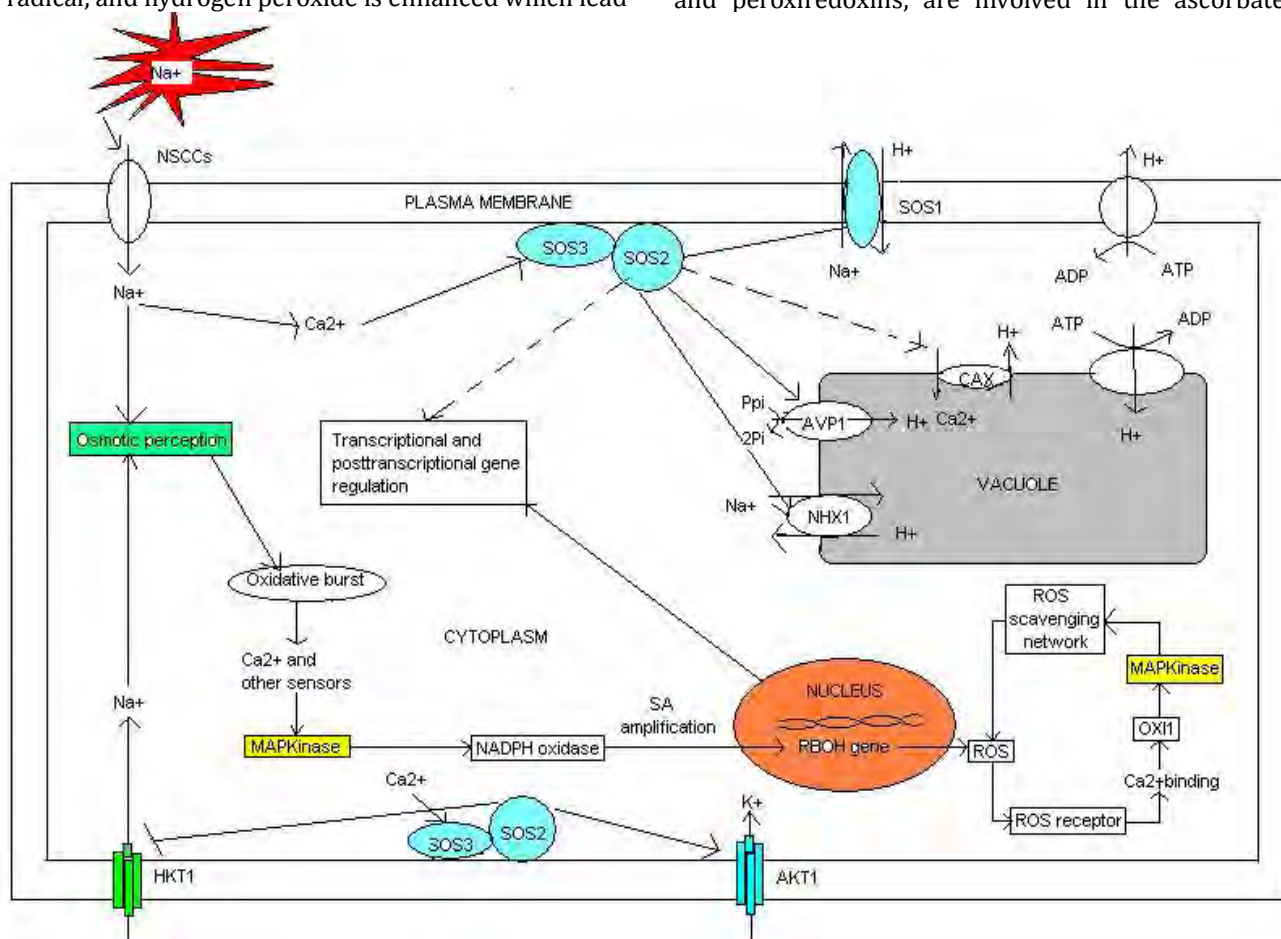


**Fig. 2**: Proposed model showing the possible survival strategies of plants under adverse environmental conditions in reference to salinity stress: Na+ is transported into the cytosol by non- selective cation channel (NSCCs) and HKT1 (low affinity sodium transporter). Salt overly systems (SOS 1, SOS 2 AND SOS 3) are involved into ion homeostasis through cytosolic $Ca^{2+}$. Vacuolar compartmentalization of $Na^+$ is performed by NHX1 and CAX1 (an $H^+$/$Ca^+$ antiporter), Salicylic acid (SA) induces ROS system (modified from Mittler *et al.*, 2004) through a serine/ threonine protein kinase (OX 1) and MAP kinases for removal of ROS stress

glutathione cycle (a pathway that allows the scavenging of superoxide radicals and $H_2O_2$). These include APX, dehydroascorbate reductase, monodehydroascorbate reductase and GR (Fazeli *et al.*, 2007). Most of the Ascorbate-glutathione cycle enzymes are located in the cytosol, stroma of chloroplasts, mitochondria and peroxisomes (Jiménez *et al.*, 1998). APX is a key antioxidant enzyme in plants whilst glutathione reductase has a central role in maintaining the reduced glutathione pool during stress. Two GR complementary deoxyribonucleic acids have been isolated; one type encoding the cytosolic isoforms and the other encoding GR proteins dual-targeted to both chloroplasts and mitochondria in different plants as shown in Fig. 2 (Chew *et al.*, 2003).

Among enzymatic mechanisms, SOD plays an important role, and catalyzes the dismutation of two molecules of superoxide into $O_2$ and $H_2O_2$; the first step in ROS scavenging systems. The transcript of some of the antioxidant genes such as glutathione reductase or APX was higher during recovery from a water deficit period and appeared to play a role in the protection of cellular machinery against damage by ROS (Ratnayaka *et al.*, 2003).

A superoxide radical has a half-life of less than 1 sec and is rapidly dismutated by SOD into $H_2O_2$, a product that is relatively stable and can be detoxified by catalase and POX (Apel and Hirt, 2004). These metalloenzymes constitute an important primary line of defense of cells against superoxide free radicals generated under stress conditions. Therefore, increased SOD activity is known to confer oxidative stress tolerance (Pan *et al.*, 2006). Oxidative damage in the plant tissue is alleviated by a concerted action of both enzymatic and non-enzymatic antioxidant systems. These include β-carotenes, ascorbic acid, α-tocopherol, reduced glutathione and enzymes including SOD, POX, APX, catalase, polyphenol oxidase and GR (Hasegawa *et al.*, 2000; Prochazkova *et al.*, 2001). Carotenes form a key part of the plant antioxidant defense system (Wahid, 2007), but they are very susceptible to oxidative destruction.

### 3.4. Salicylic acid and protein kinases

The calcium-dependent protein kinases in higher plant cells are an important group of calcium sensors that decode calcium ion signals in plant cells (Cheng *et al.*, 2002). As a family of unique serine/threonine kinases in higher plants, they perform diverse and important functions in plant signal transduction, such as salt overly-sensitive 3-like proteins (Zhu, 2002) or casitas B-lineage lymphoma and calcium-dependent

protein kinases may further transduce stress-induced calcium signals (Luan *et al.*, 2002). Mishra *et al.* (2006) also reported that signaling for cell division and stress responses in plants is mediated through monoammonium phosphate kinases, and even auxins also utilize a monoammonium phosphate kinase pathway for its action.

Plants possess sophisticated protection mechanisms to cope with various environmental stresses such as cold, freezing, heat, drought, ozone, UV light, salinity, osmotic shock, and mechanical wounding (Shinozaki and Yamaguchi-Shinozaki, 2000; Orozco-Cardenas *et al.*, 2001). Accumulating evidences indicate that plants rapidly activate MAPKs when exposed to multiple abiotic stress stimuli (Ligterink and Hirt, 2001). Mitogen activated protein kinase 4 (MPK4) has been identified as another key component involved in mediating the antagonism between SA and JA mediated signaling in *Arabidopsis*. The *Arabidopsis* mpk4 mutants show elevated SA levels, constitutive expression of SA-responsive PR genes and increased resistance to Pst. In contrast, the expression of JA-responsive genes and the resistance to *A. brassicicola* were found to be impaired in mpk4 mutants. These results indicate that MPK4 acts as a negative regulator of SA signaling and positive regulator of JA signaling in *Arabidopsis*. An osmotic stress activated SAIPK (MAPK family) was observed in tobacco cells which upregulated the activity of abscisic aldehyde oxidase in *Solanum lycopersicum* L. during ABA biosynthesis (Singh and Gautam, 2013).

SA induces acidic pathogen-related (PR) genes and inhibits basic PR genes, whereas JA does the opposite. SA also reduced the synthesis of tomato proteinase inhibitors. Antagonistic interactions between SA and JA affect the expression of PR protein genes in tomato. Jumali *et al.* (2011) showed that most genes responding to acute SA treatment are related to stress and signaling pathways which eventually led to cell death. This include genes encoding chaperone, heat shock proteins (HSPs), antioxidants and genes involved in secondary metabolite biosynthesis, such as sinapyl alcohol dehydrogenase (SAD), cinnamyl alcohol dehydrogenase (CAD) and cytochrome P450 (CYP 450). Several methods of application (soaking the seeds prior to sowing, adding to the hydroponic solution, irrigating, or spraying with SA solution) have been shown to protect various plant species against abiotic stress factors by inducing a wide range of processes involved in stress tolerance mechanisms (Horvath *et al.*, 2007).

Lipid peroxidation and membrane permeability, which were increased by salt stress, were lower in SA treated plants (Horvath *et al.*, 2007). SA treatment was

accompanied by a transient increase in the $H_2O_2$ level. As seed treatment with $H_2O_2$ itself had an alleviating effect on the oxidative damage caused by salt stress in wheat plants (Wahid, 2007), it seems possible that SA may exert its protective effect partially through the transiently increased level of $H_2O_2$. Root drenching with 0.1 mM SA protected tomato (*L. esculentum*) plants against 200 mM NaCl stress. It increased the growth and photosynthetic rate of the plants, as well as the transpiration rate, stomatal conductance and reduced electrolyte leakage by 32%. The endogenous level of SA increased under salt stress in rice seedlings and the activity of the SA biosynthetic enzyme, benzoic acid 2-hydroxylase, was induced (Sawada *et al.*, 2006). Treatment with SA essentially diminished the alteration of phytohormones levels in wheat seedlings under salinity. It was found that the SA treatment caused accumulation of both ABA and IAA in wheat seedlings under salinity. However, the SA treatment did not influence on cytokinin content. Thus, protective SA action includes the development of antistress programs and acceleration of normalization of growth processes after removal of stress factors. The results obtained in the last few years strongly argue that SA could be a very promising compound for the reduction of the abiotic stress sensitivity of crops, because under certain conditions it has been found to mitigate the damaging effects of various stress factors in plants.

## 4. Conclusion and Perspectives

The essential feature of plant survival to changing environmental conditions is their ability to observe the fluctuations in the action of biotic and abiotic components. We have to make great progress in understanding the responses of plants to biotic and abiotic stresses in regards to physiological, biochemical and molecular limitations of plants. SA is one of the specific plant hormone that goes beyond the defense reaction in plant immunity and response to abiotic stresses. Phytohormonal cross talk signaling provides fundamental knowledge on plant immune system. Concentration based application of SA in plants may bring some potential practical utilization. For example, manipulating the tissue level of SA in plants may be a promising area for the importance of biotechnology to crop protection and high yield. Increase in endogenous SA may be due to increase in its biosynthesis or blocking the expression of genes involved in SA metabolism. This article will help in developing a new concept and insight about the role of SA in growth regulation, gene induction and signaling of various metabolic pathways in plants under adverse environmental conditions.

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