Chapter 2
Salicylic Acid: Physiological Roles in Plants

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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.

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

SA, 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. Plant phenolics were categorised as secondary metabolites and relatively treated as of low importance in plant metabolism but due to the passage of time this concept changed with the discovery that phenolics play important roles in plant metabolism. For example, phenolics are involved in lignin biosynthesis; others serve as allelopathic compounds, regulate plant responses to abiotic stimuli, or play critical roles in plant disease resistance either by functioning as preformed or inducible antimicrobial defence compounds termed phytoalexins or by signalling defence activation (Humphreys and Chapple 2002; Raskin 1992).

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

2 Physiological Responses of SA

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

2.1 Plant Growth and Development

Growth and development of plants, like all organisms, is regulated by various internal external stimuli. In recent years, SA has been in focus of intensive research due to its crucial role in the regulation of physiological and biochemical processes during the entire life span of the plants and plays key roles in regulating their growth and productivity (Arberg 1981). The role of SA in seed germination has been debatable as there are inconsistent reports suggesting that it can either inhibit germination or increase seed vigour. The reported contradictory effects can be related to the SA concentrations employed. In *Arabidopsis thaliana*, SA concentrations >1 mM delay or even inhibit germination (Rajou et al. 2006). In barley, doses >0.250 mM SA inhibit seed germination (Xie et al. 2007), while in maize germination is completely inhibited by SA doses ranging from 3 to 5 mM (Guan and Scandalios 1995). The effect of SA as a negative regulator of seed germination is probably due to an SA-induced oxidative stress. In *Arabidopsis* plants treated with SA (1–5 mM), hydrogen peroxide (H_2O_2) levels increase up to 3-fold as a result of increased activities of Cu, Zn-superoxide dismutase and inactivation of the H_2O_2-degrading enzymes, catalase and ascorbate peroxidase (Rao et al. 1997). Enhanced germination and seedling growth were recorded in wheat, when the grains were subjected to pre-sowing seed-soaking treatment in SA (Shakirova 2007). Fariduddin et al. (2003) reported that the dry matter accumulation was significantly enhanced in *Brassica juncea*, when lower concentrations of SA were sprayed. However, higher concentrations of SA had an inhibitory effect.

In another study, Hayat et al. (2005) showed that the leaf number, fresh and dry mass per plant of wheat seedlings raised from the grains soaked in lower concentration (10^{-5} M) of SA, increased significantly. Similar growth promoting responses were generated in barley seedlings sprayed with SA (Pancheva et al. 1996). Khodary (2004) observed a significant increase in growth characteristics, pigment contents and photosynthetic rate in maize, sprayed with SA. The exogenous SA application also enhanced the carbohydrate content in maize (Khodary 2004). Hussein et al. (2007) in their pot experiment sprayed salicylic acid to the foliage of wheat plants, irrigated with Mediterranean sea water and reported an enhanced productivity due to an improvement in all growth characteristics including plant height, number and area of green leaves, stem diameter and dry weight of stem, leaves and of the plant as a whole.

In the year 1989, Carswell et al. reported that acetyl SA can promote colony formation in maize protoplasts suggesting a role for SA in the regulation of the cell cycle. Xyloglucan endotransglucosylase/hydrolase (*XTH*) genes encode enzymes that are implicated in cell wall loosening and cell expansion (Rose et al. 2002). Arabidopsis contains 33 *XTH* genes in its genome (Yokoyama and Nishitani 2001). Among 33 *XTH* genes, expression levels of *XTH*8, *XTH*17 and *XTH*31 were strongly down-regulated in both *cpr*5 and *mpk*4 but did not change in *nahG* (Miura et al. 2010). Reverse transcription–PCR (RT–PCR) results indicated that *XTH*8 and *XTH*31, but not*XTH*17, were down-regulated in *siz*1 and expression of *XTH*8and *XTH*31 was recovered in *nahGsiz*1-2 (Miura et al. 2010). Moreover, expression level of *XTH*24 (MERI5), a potential target for ANGUSTIFOLIA (*AN*), which regulates the width of leaves (Kim et al. 2002) and may also play a role in leafmorphogenesis at the early stage (Verica and Medford 1997). Thus, *SIZ*1 regulates SA-dependent *XTH*8 and *XTH*31 expression, but may not be involved in AN-dependent regulation of cell elongation (Miura et al. 2010).

2.2 Photosynthetic Machinery

SA has been established as an important regulator of photosynthesis, water relations and metabolic aspects of plants, depending on its analogues, concentrations, mode of application and plant type. SA is known to affect leaf and chloroplast structure (Uzunova and Popova 2000), stomatal closure (Mateo et al. 2004; Melotto et al. 2006), chlorophyll and carotenoid contents (Chandra and Bhatt 1998; Fariduddin et al. 2003), and the activity of enzymes such as Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) and carbonic anhydrase (Slaymaker et al. 2002; Hayat et al. 2012; Yusuf et al. 2008, 2012). However, high SA concentrations (1–5 mM) cause a reduction in the photosynthetic rate and Rubisco activity in barley plants (Pancheva et al. 1996), and reduce chlorophyll contents in cowpea, wheat, and *Arabidopsis* (Rao et al. 1997; Chandra and Bhatt 1998; Moharekar et al. 2003). The decline of Rubisco activity was attributed to a 50 % reduction in protein levels, compared with non-treated plants (Pancheva and Popova 1998), while total soluble protein decreased by 68 %. Exogenously applied SA induces alterations in leaf anatomy that consist of reduced width of the adaxial and abaxial epidermis, and of the mesophyll tissue (Rivas-San and Piasencia 2011). Such changes correlate ultrastructurally with an increase in chloroplast volume, swelling of grana thylakoids, and coagulation of the stroma (Uzunova and Popova 2000). Thus, the diminished photosynthetic activity at high concentrations of SA is due to its effects on the thylakoid membranes and light-induced reactions linked to them. Hayat et al. (2005) reported that the pigment content was significantly enhanced in wheat seedlings, raised from the grains pre-treated with lower concentration (10^{-5} M) of SA, whereas, higher concentrations did not prove to be beneficial. Besides seed-soaking treatment, the foliar application of SA also proved to be equally fruitful in increasing the pigment contents in *Brassica napus* (Ghai et al. 2002). Similar results were obtained when the plants of *Brassica juncea* were sprayed with lower concentration (10^{-5} M) of SA, where, the chlorophyll content was significantly enhanced (Fariduddin et al. 2003). Contrary to these observations, a reduction in chlorophyll content was observed in plants pre-treated with SA (Anandhi and Ramanujam 1997; Pancheva et al. 1996). Moharekar et al. (2003) reported that salicylic acid activated the synthesis of carotenoids and xanthophylls and also enhanced the rate of de-epoxidation with a concomitant decrease in chlorophyll pigments and chlorophyll a/b ratio in wheat and moong. Exogenous application of SA enhanced the net photosynthetic rate, internal CO_2 concentration, water use efficiency, stomatal conductance and transpiration rate in *Brassica juncea* (Fariduddin et al. 2003). Further, Khan et al. (2003) reported an increase in transpiration rate and stomatal conductance in response to foliar application of SA and other salicylates in corn and soybean. In another study carried out on soybean, foliar application of salicylic acid enhanced the water use efficiency, transpiration rate and internal CO_2 concentration (Kumar et al. 2000).

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

2.3 Nitrate Metabolism

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

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

Martinez-Abarca et al. (1998) showed SA accumulated in alfalfa roots, inoculated with a *nodC* mutant of *Sinorhizobium meliloti* that was unable to synthesize the lipochitin nod signal required for infection. This report also showed that exogenous addition of SA resulted in both reduced and delayed nodule formation on alfalfa roots inoculated with wild-type *Sinorhizobium meliloti*. Subsequently, Bueno et al. (2001) showed a decrease in antioxidant enzyme activities and an increase in H_2O_2 accumulation in alfalfa roots following inoculation with a *Sinorhizobium meliloti nodC* mutant, as well as an increase in lipoxygenase activity after inoculation with the wild-type strain.

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

2.4 Ethylene Production

The plant hormone, ethylene has been reported to affect a diverse array of plant growth and developmental processes including germination, senescence and abscission of flowers and leaves, fruit ripening as well as the response to a wide variety of stresses such as pathogen attack and drought (Abeles et al. 1992). The induction of ethylene biosynthesis takes place by a wide variety of stimuli, including wounding, pathogen attack, various stresses, mechanical stimulus and by hormones such as salicylic acid (Mattoo and Suttle 1991; Abeles et al. 1992; Raskin 1992). Recently, the survey of literature revealed that SA has been shown to interfere with the biosynthesis and/or action of ethylene in plants (Raskin et al. 1990). 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 revealed a significant (positive or negative) correlation either for up or down regulated genes. The uptake of phosphate (Glass 1973) and subsequently that of potassium (Glass 1974) by barley roots was reduced by SA. However, the inhibition of the absorption of potassium by oat roots, under the impact of SA, was dependent on the pH and the concentration of the element in the medium. This inhibition was more prominent at lower pH, suggesting higher activity of protonated form of salicylic acid (Harper and Balke 1981; Gordon et al. 2002). SA also caused the collapse of the transmembrane electrochemical potential of mitochondria and the ATP dependent proton gradient of tonoplast enriched vesicles (Macri et al. 1986).

2.6 Heat Production

Heat production, thermogenesis authenticates the discovery of SA as an endogenous plant hormone. Initial findings proved that SA triggers a dramatic increase in the production of metabolic heat and insect-attracting chemicals in the thermogenic inflorescence of *Arum lilies* (Raskin 1992) and possibly other plants also (Raskin et al. 1990). In *Sauromatum guttatum* Schott (voodoo lily), a 100-fold increase in SA precedes with the onset of thermogenesis in the spadix (Vlot et al. 2009). The induction of thermogenesis by SA is very specific: of 33 SA analogues tested, only 2, 6-dihydroxybenzoic acid and aspirin induce this response. SA stimulates thermogenesis primarily by increasing the activity of alternative respiratory pathway in mitochondria. Unlike the cytochrome respiratory pathway, electron flow through the alternative respiratory pathway generates ATP at only one site with the unused potential energy being released as heat (Vlot et al. 2009). Remarkably, SA treatment also induces alternative oxidase expression and increased alternative respiration in tobacco, a nonthermogenic plant (Norman et al. 2004). Exogenously applied SA treatment improved thermotolerance and heat acclimation in mustard seedlings (Dat et al. 1998). A similar response was also observed in potato plantlets, raised from the cultures, supplemented with lower concentrations of acetyl salicylic acid (Lopez-Delgado et al. 1998). Larkindale and Huang (2004) pointed out that the enhanced heat tolerance in plants of *Agrostis stolonifera*, pre-treated with salicylic acid was due to the protection of plants from oxidative damage. These authors further reported that the pre-treatment with salicylic acid had no effect on POX activity, whereas, the CAT activity declined, compared to control. Foliar spray of lower concentrations of salicylic acid conferred heat tolerance to mustard. Further this treatment accompanied with hardening at 45 °C for 1 h enhanced H_2O_2 level and also reduced CAT activity, thereby increasing the potential of plants to withstand the heat stress (Dat et al. 1998).

2.7 Flowering

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

2.8 Senescence

Plant senescence is a phenomenon that resembles age of the plant that closely connects with cell death. It is developmentally well defined that optimizes the growth and reproductive capacity of plants by recycling of resources from senescing leaves into young leaves or seeds. After well documented the importance of role of SA in photosynthesis and flowering, it is not unanticipated that this plant hormone is also involved in regulation of senescence. This process is characterized by yellowing of leaves due to chlorophyll degradation (Vogelmann et al. 2012) and increased ROS levels (Rivas-San and Plasencia 2011). It is believed that these events are due to SA accumulation. In *Arabidopsis* senescent leaves, SA levels increase 4-fold at the mid-senescent stage. Consistent with this observation, Arabidopsis plants affected in SA biosynthesis, such as the transgenic NahG and the mutant pad4, or with a disrupted SA signalling pathway, such as npr1, exhibit altered senescence patterns that include delayed yellowing and reduced necrosis compared with wild-type plants (Morris et al. 2000). Moreover, senescence is escorted by important changes in gene expression, and SA paly pivotal role in successful execution of this process. Transcripts of several SAGs, such as *SAG*12, are considerably reduced or undetectable in SA-deficient *Arabidopsis* plants (Morris et al. 2000). In addition this, SA activates the expression of the *Arabidopsis* senescence-related genes *αVPE, χVPE, WRKY*6, *WRKY*53*, and SEN*1 that encode two vacuolar processing enzymes, two transcription factors, and a protease, respectively (Robatzek and Somssich 2001; Miao et al. 2004; Schenk et al. 2005). The involvement of the SA signalling pathway in senescence was confirmed through a detailed microarray analysis in *Arabidopsis* senescent leaves (Buchanan-Wollaston et al. 2005). Almost 20 % of the up-regulated genes during senescence show at least 2-fold reduced expression in SA-deficient NahG transgenic plants. Most of the senescence enhanced genes that are dependent on the SA pathway encode kinases, transferases, and hydrolases, but their function in senescence progression remains to be elucidated. Although a great deal of effort has been put into identifying the signalling factors required for senescence regulation, further research must determine whether SA is involved in different stages of senescence, and the interconnecting networks with other phytohormones that promote (ABA, JA, an ET) or delay (CKs and GAs) senescence.

3 Effect of SA on Yield

The credibility on any exogenously sourced plant hormones evaluate in terms of biological yield. SA is known to be a natural signal molecule has been shown to play an important role in regulating various physiological processes in plants including yield. Yildirim and Dursan (2009) revealed that foliar application of SA showed positive effect on early yield and total yield and also proposed that highest yield occurred in 0.50 mM SA treatment and also recommended in order to improve yield. Sharafizad et al. (2012) showed that highest grain yield was obtained with application of 0.07 mmol SA. It is believed that increasing the crop yield might be due to delayed senescence of plant organs (particularly leaves and flowers) in response to exogenous SA (Imran et al. 2007) that will automatically help the plant in extending the duration of photosynthetically active sites and also prevent the premature loss of flowers and fruits. This consequently resulted in the observed increase in the number of crop yield. Moreover, Marschner (2003) that phytohormones increase the degree of sink at the level of seeds, directing the flow of metabolites to the developing seeds consequent to an improvement in the seed mass and seed yield per plant at harvest.

4 Conclusions

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

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