Chapter 4
Salicylic Acid

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Introduction

Fresh fruits and vegetables are highly perishable after harvest which causes a significant loss of the harvested produce. Synthetic chemicals and fungicides are repeatedly used for several years to minimize the decay and postharvest loss of fruits and vegetables. However, indiscriminate and continuous application of chemicals over the produce and its harmful effects on human health and environment lead the scientists to search safe compounds that might be helpful in preserving the quality of harvested produce. Moreover, repeated application of synthetic fungicides may develop pathogen resistance against the synthetic fungicides.

Salicylic acid (SA) or monohydroxy benzoic acid belongs to a group of phenolic compounds which is present ubiquitously throughout the plant kingdom. It is an endogenous signal molecule, involved in regulating a variety of physiological processes in plants. SA plays an important role in regulating several plant developmental processes like thermogenesis, photosynthesis, respiration, transpiration, stomatal closure, seed germination, cell growth, sex polarization, ion uptake and transport, disease resistance, senescence-associated gene expression, and crop yield (Klessig and Malamy 1994; Clarke et al. 2004; Morris et al. 2000; Rajou et al. 2006; Harper and Balke 1981; Khan et al. 2003). SA is a major component of signal transduction

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pathway which plays a pivotal role in inducing multiple mode of resistance to plants (Asghari and Aghdam 2010). SA has also been reported to involve in activating local and systemic disease resistance in response to pathogen attack (Enyedl et al. 1992; Alverez 2000). Moreover, it also modulates the response of plant to various abiotic stresses like drought, salinity, heat shock, chilling stress, and UV light (Ding and Wang 2003; Ding et al. 2001). During recent years, SA has received particular attention in extending shelf life and preserving postharvest quality of fresh horticultural produce due to its anti-ripening, anti-senescence properties and enhancing resistance to different biotic and abiotic stresses (Table 4.1).

Brief History of Salicylic Acid

During fourth century B.C., women were encouraged to chew leaves of willow plant to relieve pain during childbirth (Raskin 1992). Despite wide popularity of willow leaves and bark as a folk remedy of pain, its medicinal properties were not studied until mid-1700 by Reverend Edward Stone in Oxfordshire, England. In the year 1828, Johann A. Buchner, a German scientist, extracted and purified a small quantity of a yellowish substance, and he called it salicin. Later in 1838 an Italian chemist, Raffaele Piria, split salicin into a sugar and an aromatic compound which could be converted to acid and named acide salicylice or salicylic acid (Vlot et al. 2009). In the year 1859, first chemical synthesis of SA was carried out by Hermann Kolbe and his coworkers which led large-scale production of SA for medicinal use. However, its unpleasant taste and long-term side effects restricted its wide use. Later, an employee of Bayer pharmaceutical company, Felix Hoffmann, identified that acetylation of SA yielded a compound which is better tolerated without affecting its desirable qualities. In the year 1899, this acetyl salicylic acid was given the trade name of aspirin for its marketing as a pain-killer medicine.

Salicylic Acid Biosynthesis and Metabolism

In plants, biosynthesis of SA takes place via two distinct pathways that involve the primary metabolite chorismate (Garcion and Métraux 2006). In one pathway, L-phenylalanine derived from chorismate is converted into SA either via benzoate intermediates or from coumaric acid intermediates through a series of enzymatic reactions. In another pathway, chorismate is converted to isochorismate by the enzyme isochorismate synthase (ICS) which later converted to SA by the enzyme isochrismate pyruvate lyase (IPL) (Strawn et al. 2007; Verberne et al. 2000; Wildermuth et al. 2001) (Fig. 4.1). It has been reported that SA produced from chorismate in chloroplasts is responsible for inducing local and systemic acquired resistance in plants (Wildermuth et al. 2001). In the first pathway, L-phenylalanine is first converted to cinnamic acid by the enzyme phynylalanine ammonia lyase (PAL). Two routes for the conversion of cinnamic acid to SA exist which differ in

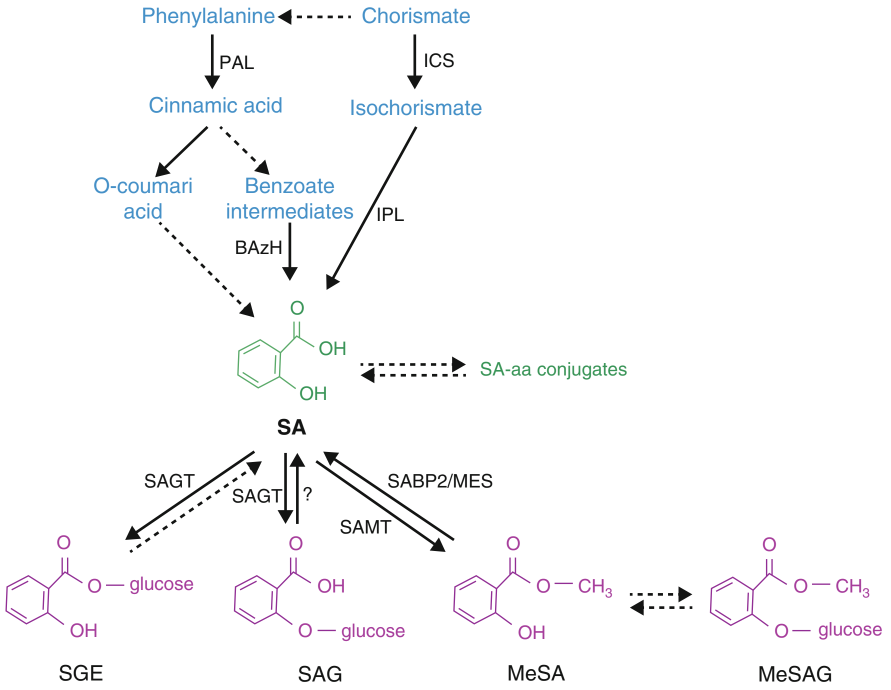

Fig. 4.1 Biosynthesis pathway and metabolism of salicylic acid. Abbreviations: *PAL* phenylalanine ammonia lyase, *ICS* isochorismate synthase, *IPL* isochorismate pyruvate lyase, *BA2H* benzoic acid-2-hydroxylase, *SA* salicylic acid, *SAGT* SA glucosyltransferase, *aa* amino acid, *SAMT* SA methyltransferase, *SABP*$_2$ SA-binding protein 2, *MES* methyl esterase, *SGE* salicyloyl glucose ester, *SAG* SA *O*-β-glucoside, *MeSA* methyl salicylate, *MeSAG* methyl salicylate *O*-β-glucoside (source: Vlot et al. 2009)

hydroxylation of aromatic ring. In one route, side chain of cinnamic acid is oxidized to form benzoic acid, which later undergoes hydroxylation in *ortho* position to form SA. Such biosynthetic pathway of SA has been reported in tobacco (Yalpani et al. 1993) and rice (Silverman et al. 1995). In another pathway, cinnamic acid first hydroxylated into *ortho*-coumaric acid followed by oxidation of the side chain takes place to form SA (Sticher et al. 1997). In this, enzyme trans-cinnamate-4-hydroxylate catalyzes conversion into SA which was identified in pea seedling (Russell and Conn 1967), *Quercus pedunculata* (Alibert and Ranjeva 1971, 1972), and *Melilotus alba* (Gestetner and Conn 1974). According to earlier studies on tobacco, synthesis of SA was reported to occur from free benzoic acid however; later results revealed that benzoyl glucose, a conjugated form of benzoic acid, is the precursor of SA (Yalpani et al. 1993; Chong et al. 2001).

Salicylic acid forms conjugates with different molecules either by glycosylation or by esterification (Popova et al. 1997). A major portion of SA produced in plants is converted into SA *O*-β-glucoside (SAG) by the enzyme SA-glucosyltransferase (SAGT) which has been found in suspension cultures of *Mallotus japonicus* (Tanaka et al. 1990) and roots of *Avena sativa* seedlings (Balke and Schulz 1987; Yalpani

Table 4.1 Various effects of salicylic acid on fruits and vegetables during postharvest storage

Crop	Effects of salicylic acid (SA)	References
Chinese water chestnut	Reduced browning, maintained eating quality, reduced disease incidence and activities of PPO, POD, and PAL enzymes	Peng and Jiang (2006)
Tomato	Reduced weight loss, decay percentage, delayed changes in total soluble solids, titratable acidity, sugar accumulation, chlorophyll degradation, carotenoids accumulation, enhanced storage life, alleviated chilling injury	Pila et al. (2010), Aghdam et al. (2012)
Sweet cherry	Delayed ripening and associated changes in firmness, acidity, color, enhanced total phenolics, anthocyanins and antioxidant capacity, induced disease resistance, increased activities of CAT, glutathione peroxidase, chitinase and β-1,3-glucanase, PAL and POD	Valero et al. (2011), Chan et al. (2008), Xu and Tian (2008), Yao and Tian (2005)
Sugar apple	Reduced respiration, ethylene production rates, softening and decay rates, increased activities of SOD, POD, CAT, APX, and decreased activity of LOX enzymes	Mo et al. (2008)
Strawberry	Superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), and ascorbate peroxidase (APX), Reduced weight loss, ethylene production, fungal decay, maintain higher firmness and vitamin C	Babalar et al. (2007), Shafiee et al. (2010)
Pomegranate	Alleviated chilling injury, reduced PAL activity, respiration rate, and preserved phenolics, anthocyanins, antioxidant capacity, sugars, and organic acids	Sayyari et al. (2009, 2011)
Plum	Reduced chilling injury, respiration and ethylene production rates, disease incidence, reduced PPO and POD activity	Luo et al. (2011)
Pineapple	Reduced internal browning, inhibited PPO and PAL activities, delayed decline in ascorbic acid content	Lu et al. (2011)
Pepper	Increased cuticle thickness of fruit pericarp, vitamin C, carotenoids content, invertase activity, and reduced POD activity	Elwan and El-Hamahmy (2009)
Asparagus	Improved color and maintained chlorophyll, phenolics, flavonoid, ascorbic acid content, and antioxidant activity	Wei et al. (2011)
Banana	Delayed ripening, decreased fruit softening, pulp:peel ratio, reducing sugar content, respiration rate, and enzyme activity of invertase, cellulase, xylanase, and polygalacturonase	Srivastava and Dwivedi (2000)
Mango	Alleviate chilling injury, reduce weight loss, fruit softening, disease incidence, PME and PG activities, and preserved carotenoids, phenolics, and antioxidant capacity of fruit	Barman and Asrey (2014)
Litchi	Reduced pericarp browning, decay percentage, electrolyte leakage, weight loss, PPO activity and maintained higher anthocyanin content	Kumar et al. (2013)

PPO polyphenol oxidase, *POD* peroxidase, *PAL* phenylalanine ammonia lyase, *SOD* superoxide dismutase, *CAT* catalase, *APX* ascorbate peroxidase, *LOX* lipoxygenase et al. 1992). In Arabidopsis, two SAGT enzymes have been found: one converts SA into SAG while the other forms less abundant SA derivative, salicyloyl glucose ester (SGE) (Dean and Delaney 2008). Synthesis of SA takes place in the chloroplast whereas in tobacco SAGT is present in cytosol (Dean et al. 2005; Garcion et al. 2008; Strawn et al. 2007). SAG is transported into vacuole from cytosol, where it remains as inactive storage that later converted to SA (Dean and Mills 2004; Dean et al. 2005).

Role of Salicylic Acid in Postharvest Management of Horticultural Crops

Effect on Ethylene Biosynthesis

Ethylene plays an important role in the postharvest physiology of horticultural crops by inducing fruit ripening and senescence. During fruit ripening, a series of biochemical and physiological changes (Table 4.2) take place that initiate the processes of senescence. Ethylene is produced from L-methionine that includes the intermediates SAM (S-adenosyl methionine) and ACC (1-aminocyclopropane-1-carboxylic acid) (Fig. 4.2). The two enzymes responsible for the conversion of SAM to ACC and ACC to ethylene are ACC synthase and ACC oxidase, respectively. SA decreases the ethylene biosynthesis by reducing the activity of ACC synthase and/or ACC oxidase enzymes. Exogenous application of SA and its derivative acetyl salicylic acid (ASA) significantly decreases ethylene production in cultured pear cell, apple and pear fruit tissue, mung bean hypocotyl, cell suspension culture of carrot, and several fruit crops (Babalar et al. 2007; Romani et al. 1989; Leslie and Romani 1988). In banana, exogenous application of SA delayed ripening of fruit probably through reducing ethylene production (Srivastava and Dwivedi 2000). Similarly in kiwifruit, postharvest application of acetyl salicylic acid (1.0 mmol/L) decreased the endogenous production of ethylene during early stages of fruit ripening (Zhang et al. 2003). In strawberry fruit, preharvest application of SA (2 mmol/L) at three stages of vegetative growth, fruit development

Table 4.2 Changes associated with fruit ripening (source: Wills et al. 2007)

Changes in color
Changes in respiration rate
Changes in ethylene production rate
Softening of fruit due to changes in composition of pectic substances
Changes in carbohydrate composition
Changes in organic acid
Changes in protein
Production of flavor volatiles
Development of wax on peel

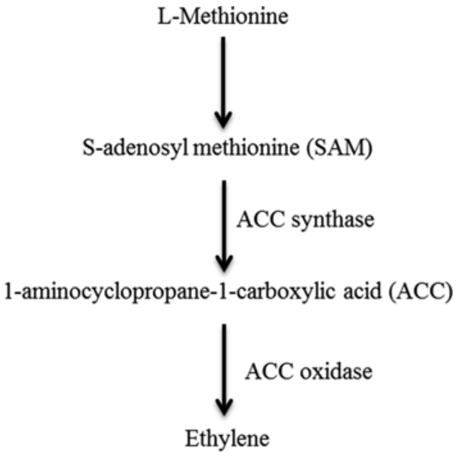

Fig. 4.2 Biosynthesis pathway of ethylene

stage, and after harvest was found effective in reducing ethylene production. However, single application of SA at postharvest stage was found more effective than its application at vegetative growth and fruit development stage (Babalar et al. 2007). Application of SA in other fruits like mango, plum, and sugar apple was also reported highly effective in reducing biosynthesis of ethylene (Barman and Asrey 2014; Luo et al. 2011; Mo et al. 2008).

Effect on Fruit Firmness

With the onset of ripening, firmness of fruit decreases progressively. During this period, activities of cell wall and membrane-degrading enzymes like pectin methyl esterase (PME), polygalacturonase (PG), and lipoxygenase (LOX) increase which causes faster decrease in fruit firmness. Application of SA has been reported to reduce ethylene production, thereby reducing the activities of above cell wall and membrane-degrading enzymes (Srivastava and Dwivedi 2000; Zhang et al. 2003). A positive correlation between LOX activity and ethylene biosynthesis in fruit tissue has been reported by Marcelle (1991). Postharvest treatment of sweet cherry (‘Cristalina’ and ‘Prime Giant’) with salicylic acid (SA) or acetyl salicylic acid (ASA) at 1 mM concentration delayed loss of fruit firmness during storage under cold temperature for 20 days (Valero et al. 2011). In banana, 1000 μM SA application delayed fruit softening by reducing activities of fruit-softening enzymes, namely cellulase, polygalacturonase (PG), and xylanase (Srivastava and Dwivedi 2000). In another study, immersion treatment of banana fruit in 0.8 mmol L^{-1} SA solution for 4 h was found to be effective in maintaining higher firmness (Hui-gang et al. 2009). Barman and Asrey (2014) reported that mango fruits, when treated with SA and stored at 8 °C, maintained significantly higher firmness than control. The authors mentioned that higher fruit firmness in SA-treated fruit was attributed to lower activities of PME and PG enzymes than control. Combined application of SA with calcium chloride was also found to be effective in increasing firmness of kiwifruit during cold storage at 1 °C up to 60 days (Kazemi et al. 2011). Zhang et al. (2003) also reported a positive correlation between fruit firmness and endogenous free SA content in kiwifruit. In strawberry, application of SA (2 mM) in nutrient solution maintained higher firmness of fruit than control (Shafiee et al. 2010).

Effect on Alleviating Chilling Injury

Low-temperature storage is an effective and commercial means for extending shelf life of horticultural produce. However, fruits and vegetables of tropical and subtropical origin are prone to chilling injury (CI) while stored at low but nonfreezing temperatures below the critical point. CI causes skin pitting, discoloration of peel and flesh, shriveling and sunken lesions on the peel, uneven ripening, poor color, reduced aroma, the development of off-flavors, and increased susceptibility to fungal or bacterial decay (Nair et al. 2003; Nair and Singh 2009). As a result, market value of the fruit is affected negatively and reduces its shelf life. This CI consists of primary (reversible) and secondary (irreversible) events. In primary event, when susceptible produce are exposed to chilling temperatures, it causes phase change of membrane lipids from liquid to gel state, production of reactive oxygen species (ROS), and dissociation of enzymes and other proteins into their structural subunits (Lyons 1973; Wills et al. 2007). These ROS cause oxidative burst and damage subcellular components including membranes. Later, primary events dispose the susceptible tissues to develop secondary events, a cascade of deteriorative reactions, causing electrolyte leakage, impaired metabolic process, cell autolysis, and cell death (Parkin et al. 1989; Sevillano et al. 2009). Treatment of fruit and vegetables with SA has been reported highly effective in alleviating chilling injury during postharvest storage at low temperature. Application of SA induced expression of ROS avoidance genes and ROS scavenging genes like SOD, CAT, and APX. As a result, it increased antioxidant capacity of cells which subsequently reduced chilling injury (Asghari and Aghdam 2010) (Fig. 4.3). Moreover, it also induces synthesis and accumulation of heat-shock proteins (HSPs) which confers protection of horticultural produce against CI (Tian et al. 2007). Wang et al. (2006) reported that SA (1.0 mM) pretreatment of peach fruit alleviated CI during storage at 0 °C for 28 days. They mentioned that stress tolerance of SA-treated fruit was attributed to enhanced antioxidant systems and accumulation of HSPs (HSP101 and HSP73) in the cells. SA treatment enhanced activities of reduced-to-oxidized ascorbate ratio (AsA/DHAsA), reduced-to-oxidized glutathione ratio (GSH/GSSG), ascorbate peroxidase, and glutathione reductase in the fruit compared to control. In pomegranate, immersion treatment of fruit with 2.0 mM SA reduced CI and electrolyte leakage of fruit during low-temperature storage (Sayyari et al. 2009). Similar dose of SA was also found effective in mango (Barman and Asrey 2014). In tomato and

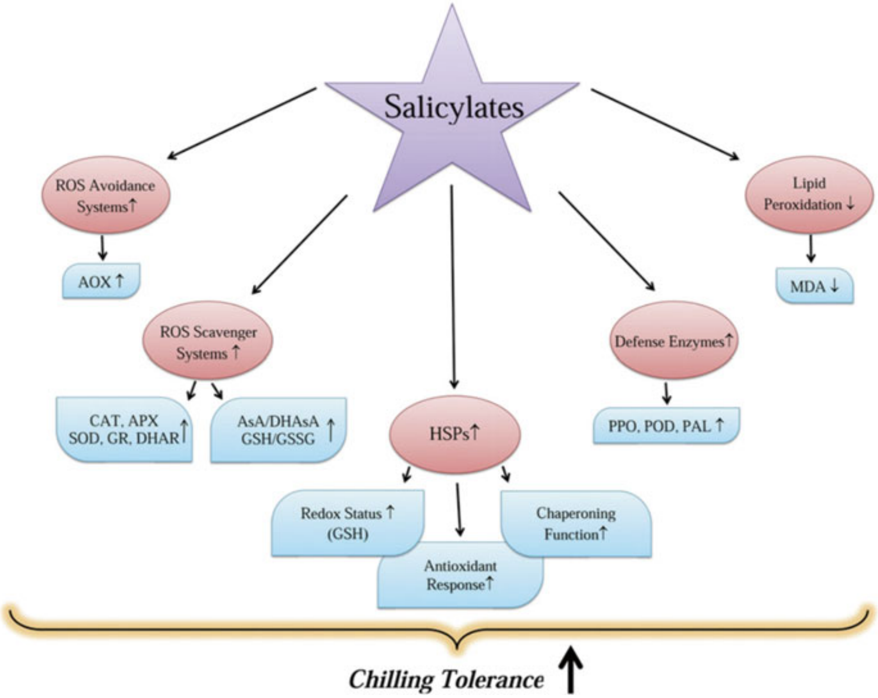

Fig. 4.3 Induction of chilling tolerance by SA (source: Asghari and Aghdam 2010)

cucumber, SA treatment reduced chilling-induced membrane lipid peroxidation and accumulation of malondialdehyde (MDA) during storage at 1 °C (Aghdam et al. 2012; Cao et al. 2009). In case of plum, SA treatment reduced CI by increasing accumulation of polyamines and reducing electrolyte leakage and MDA accumulation (Luo et al. 2011).

Effect on Reducing Disease Incidence

Plants continuously remain exposed to a variety of pathogenic attack in the environment. However, they have several inherent mechanisms to defend themselves from these pathogenic microorganisms. One such mechanism involves accumulation of large quantities of SA in response to pathogenic attack (Hayat et al. 2010). Malamy et al. (1990) reported that large amount of SA was accumulated in the leaves of tobacco mosaic virus (TMV)-resistant tobacco cultivar Xanthi when it was inoculated with TMV. Similar increase in endogenous SA was noted in cucumber plant upon infection with *Colletotrichum lagenarium*, *Pseudomonas syringae*, or tobacco necrosis virus (Metraux et al. 1990; Rasmussen et al. 1991; Smith et al. 1991). Similar to these findings, exogenous application of SA or its synthetic analogue acetyl salicylic acid (ASA) provides tolerance or reduces disease incidence in fruits and vegetables against various pathogens during postharvest storage (Malamy and Klessig 1992). When plants are attacked by the pathogen, it activates some defence mechanisms viz. local acquired resistance (LAR) and systemic acquired resistance (SAR) against the pathogens (Vlot et al. 2009). Initially, defence responses are activated at the infection site (LAR), which subsequently triggered systemic defence response to protect undamaged plant parts from invasion by the pathogen. This systemic acquired resistance (SAR) activates specific set of *PR* genes which encode for proteins with antimicrobial activity (Durrant and Dong 2004; Van Loon et al. 2006). Meena et al. (2001) reported that SA induced expression of a range of defence genes like chitinase, β-1,3-glucanase, and peroxidase. It also increases level of SA in plants which decreases expression of ascorbate peroxidase (APX) and catalase (CAT) genes that lead to increase in H_2O_2, which acts as secondary messenger for activation of LAR and SAR (Fig. 4.4) (Klessig and Malamy 1994; Tian et al. 2007). Transgenic plants and mutants in which SA signaling is impaired are not capable of developing SAR and do not show activation of *PR* genes upon infection by pathogens (Durrant and Dong 2004; Pieterse et al. 2009).

In mango, Zeng et al. (2006) reported that treatment of fruit with SA increased the activity of β-1,3-glucanase and production of H_2O_2 and superoxide radicals than control after 8 days of storage. In another study, postharvest application of SA

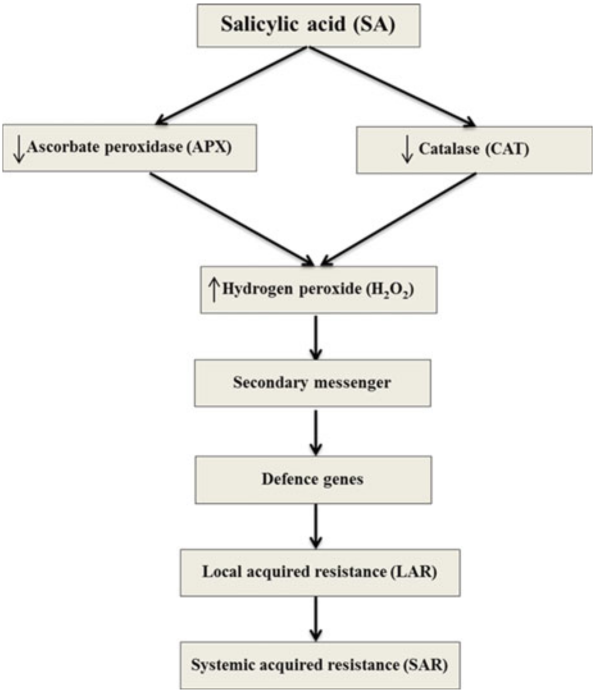

Fig. 4.4 Effect of SA on inducing disease resistance (source: Asghari and Aghdam 2010)

(2.0 mM) in mango was found highly effective in reducing disease incidence during low-temperature storage at 8 °C for up to 30 days (Barman and Asrey 2014). Immersion treatment of banana fruit in 0.8 mmol L^{-1} SA solution for 4 h reduced disease incidence (Hui-gang et al. 2009). Chan et al. (2008) reported that SA-induced disease resistance against *Penicillium expansum* in sweet cherry fruit depends upon maturity stage, the less mature fruit being more resistant to diseases. SA was found to induce disease resistance by activating antioxidant proteins like POD, CAT, and SOD. Similar response was found when sugar apple fruits were treated with SA (Mo et al. 2008). Cao et al. (2006) reported that young pear fruits, when sprayed with SA, increased activities of defensive enzymes like chitinase, POD, and PAL. In another study, treatment of SA (2.0 mM) induced disease resistance by stimulating activities of PPO, PAL, and β-1,3-glucanase in sweet cherry fruit (Qin et al. 2003; Chan and Tian 2006). In fresh-cut Chinese water chestnut, treatment with 2.0 and 4.0 mM SA completely checked disease development up to 12 days of storage (Peng and Jiang 2006). In tomato, treatment of fruit with 0.4 mM SA significantly reduced decay percentage than control (Pila et al. 2010). Preharvest treatment of strawberry plants at vegetative stage and fruit development stage followed by postharvest treatment of fruits with 1 and 2 mmol L^{-1} was found highly effective in reducing fungal decay of fruit, in a concentration-dependant manner (Babalar et al. 2007).

SA has also been reported to enhance biocontrol efficacy of antagonistic yeast. Combined application of 10 μg ml^{-1} SA with *Cryptococcus laurentii* improved the biocontrol efficacy of yeast against blue mould rot caused by *Penicillium expansum* on apple in a concentration-dependant manner (Yu and Zheng 2006). However, SA was less effective at higher or lower concentrations. Similarly in sweet cherry, 0.5 mM SA reduced the disease incidence of blue mould (*Penicillium expansum*) and alternaria rot (*Alternaria alternata*) by enhancing efficacy of antagonistic yeast *R. glutinis* (Qin et al. 2003).

Effect on Antioxidant Enzymes

Stress in plants induces generation of reactive oxygen species (ROS) such as superoxide radicals ($O_2^{\bullet -}$), hydroxyl radical ($OH^{\bullet -}$), hydroperoxyl radical ($HO_2^{\bullet}$), hydrogen peroxide (H_2O_2), and singlet oxygen ($O_2^{\bullet}$) which creates oxidative stress in plants (Elstner 1982; Halliwell and Gutteridge 1988; Asada 1994; Gille and Singler 1995; Monk et al. 1989; Prasad et al. 1999; Panda et al. 2003a, b). These ROS cause damage to the biological macromolecules such as lipids, proteins, and nucleic acids, thus altering the redox homeostasis (Smirnoff 1993; Gille and Singler 1995). To cope up with this oxidative stress, plant has two types of defence system; one includes ROS avoidance genes like alternative oxidase (AOX) while the other includes ROS scavenging genes like superoxide dismutase (SOD), catalase (CAT), ascorbate/glutathione cycle, glutathione peroxidase system, and thioredoxin system (Fig. 4.5) (Buchanan et al. 2000). Application of SA has been reported to increase the antioxidant capacity by inducing expression of AOX. In watermelon, exogenous

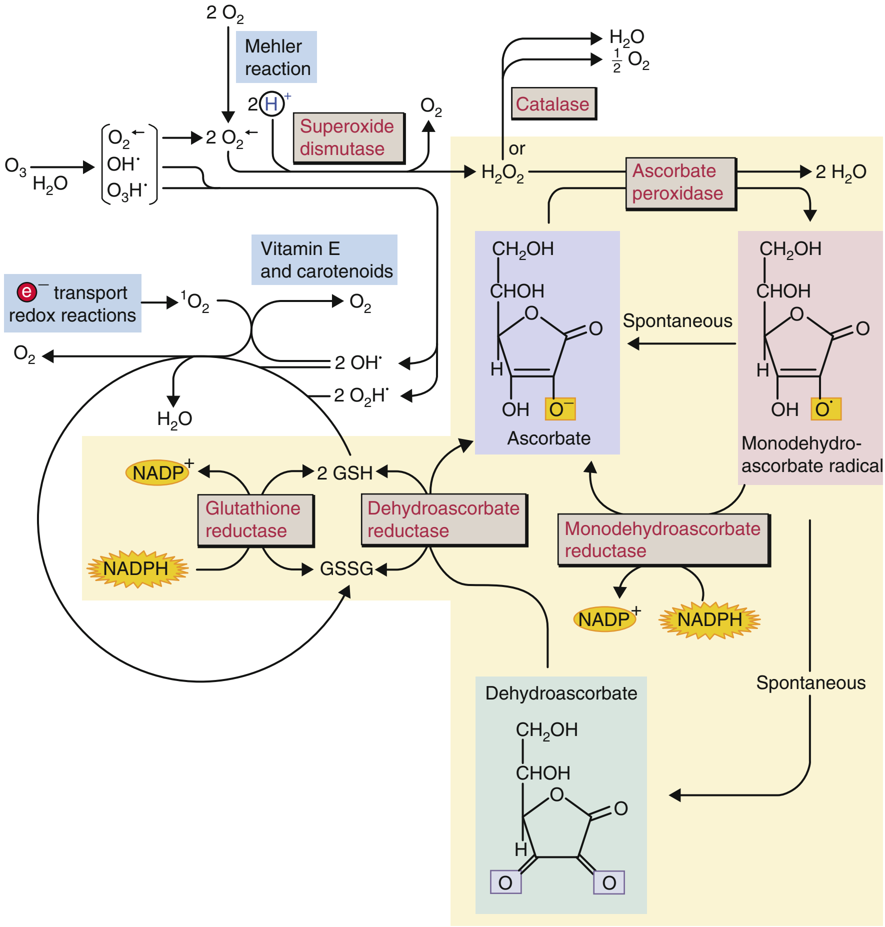

Fig. 4.5 Antioxidant systems in plant (source: Asghari and Aghdam 2010)

application of SA (1.0 mmol L^{-1}) induced the activity of antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (G-POD), and glutathione reductase (GR); however, higher concentration of SA inversely depressed the oxidative enzymes activities (Jing-Hua et al. 2008). In strawberry, SA enhanced antioxidant capacity of fruit in a concentration-dependent manner from 0 to 2 mmol L^{-1}, the highest concentration being the most effective treatment. Consequent application of SA at three different stages, viz. vegetative growth stage, fruit development stage, and postharvest stage, also proved effective in enhancing total antioxidant capacity of fruit (Asghari and Babalar 2009). In sweet cherry, postharvest treatment of fruit with SA highly inhibited CAT activity; however, it stimulated the activities of SOD and POD. This treatment also changed the expression of POD isozymes, indicating that SA directly or indirectly activates antioxidant enzymes (Tian et al. 2007). In another study, application of salicylic acid (SA) or acetyl salicylic acid (ASA) at 1 mM increased total phenolics, anthocyanins, and antioxidant activity of sweet cherry (cv. Cristalina and Prime Giant) during their postharvest storage at cold temperature (Valero et al. 2011). In banana, application of 1000 μM SA reduced activities of CAT and POD in a concentration-dependant manner (Srivastava and Dwivedi 2000); however, Huigang et al. (2009) reported that dipping of banana fruit in 0.8 mmol L^{-1} SA solution for 4 h increased the activities of SOD, CAT, and POD enzymes. In sugar apple fruit, SA increased the activities of antioxidant enzymes SOD, POD, CAT, and APX during their storage (Mo et al. 2008). In vegetables like asparagus and carrot, application of SA increased antioxidant activity during postharvest storage (Wei et al. 2011; Eraslan et al. 2007). In cucumber, treatment of fruit with SA (0.5 mM) increased activities of SOD, CAT, POD, APX, and PAL during storage under chilling stress condition (Cao et al. 2009).

Reduce Browning

Enzymatic browning of fruits and vegetables drastically reduces its nutritional value and consumer appeal. Browning mainly takes place due to oxidation of phenolic compounds by the enzyme polyphenol oxidase (PPO). In plant cells, phenolic compounds are located in the vacuoles, whereas PPO is located in the plastids (Vaughn and Duke 1984). PPO first catalyzes the hydroxylation of monophenols to colorless diphenols, which later converted to brown-colored quinone polymers (Murata et al. 1995). This reaction takes place in the presence of oxygen. Application of SA has been reported to reduce browning incidence in several fruit crops. Dipping of fresh-cut Chinese water chestnut in solution of SA (4.0 mM) highly inhibited browning of fruit by reducing the activities of PPO, POD, and PAL during storage (Peng and Jiang 2006). The bright red color of litchi fruit pericarp rapidly turns brown after harvest within a couple of days, which is a major postharvest problem in litchi. Postharvest application of 0.5 % SA by immersion method has been reported highly effective in reducing pericarp browning of litchi (Kumar et al. 2013). They have mentioned that reduced browning of fruit was due to lower PPO activity, weight loss, and electrolyte leakage in treated fruits compared to control fruit. Similarly in pineapple, preharvest SA spray and/or postharvest SA immersion treatment significantly reduced internal browning incidence and intensity by reducing PPO and PAL activity, during storage at 10 °C (Lu et al. 2011).

Effect on Sugars and Total Soluble Solids

With the onset of fruit ripening, soluble sugar content in the fruit increases by the enzyme sucrose phosphate synthase (SPS) (Hubbard et al. 1991). This enzyme is activated by ethylene that is produced in large quantities with the onset of ripening in climacteric fruit (Langenkamper et al. 1998). In tomato, SA treatment reduced total soluble solids, total sugars, and reducing and nonreducing sugars, than control. They postulated that SA delays the degradation of starch and other polysaccharides into water soluble sugars. It also slowed down the respiration and metabolic activities, and hence retarded changes of carbohydrates to sugars (Pila et al. 2010). Kiwifruits treated with MeSA 32 ml L^{-1} contained lower TSS than control during postharvest storage at low temperature (Aghdam et al. 2009). MeSA reduced ethylene production rate, thereby reducing activity of SPS enzyme and sucrose synthesis. Application of 1000 μM SA reduced activities of invertase and delayed increase in reducing sugars and decrease in nonreducing sugars in banana (Srivastava and Dwivedi 2000). Similarly, in another study, immersion treatment of banana fruit in 0.8 mmol L^{-1} SA solution for 4 h delayed conversion of starch to soluble sugars (Hui-gang et al. 2009). Furthermore, a large amount of polysaccharides are also present in the cell wall like pectins and cellulose which are broken down due to the activity of cell wall-degrading enzymes. SA was found highly effective in reducing activities of cell wall-degrading enzymes, thereby preventing significant increase in TSS content (Asghari and Aghdam 2010).

Effect on Respiration Rate

SA has been found to be effective in reducing respiration rate of fruit and vegetables. It has been reported that SA induces cyanide resistance respiration in plant cells by affecting antioxidant enzyme activity (Raskin et al. 1989). The reduction of respiration rate by SA is also due to reduced ethylene production and senescence of produce after its application. The rate of respiration is related to ethylene production and senescence; thus any factor increases the ethylene production also promotes increase in respiration rate (Asghari and Aghdam 2010). Thus, lower respiration rate after SA treatment of fruits and vegetables is mainly due to its negative effects on ACC synthase, ACC oxidase, PG, PME, and other antioxidant enzymes that decrease ethylene production and action. Moreover, increase in antioxidant activity of horticultural produce also suppresses the rate of respiration by reducing oxidative stress such as chilling injury. In sugar apple, SA reduced respiration rate by increasing antioxidant enzymes (SOD, POD, CAT, APX) and reducing ethylene production rate and superoxide radicals (Mo et al. 2008). Treatment of pomegranate fruit with ASA and plum with SA reduced respiration rate of fruit by alleviating chilling injury during storage at low temperature (Sayyari et al. 2011; Luo et al. 2011). Srivastava and Dwivedi (2000) reported that SA treatment of banana fruit reduced the rate of respiration and delayed the onset of respiratory climacteric than control fruits in a concentration-dependant manner.

Conclusion

Salicylic acid (SA), a safe phenolic compound, exhibits tremendous potential in reducing postharvest loss of fresh fruits and vegetables. Exogenous application of SA delays fruit ripening and senescence by reducing rate of respiration, ethylene production, and maintaining higher firmness. It also plays an important role in minimizing disease incidence of horticultural produce by inducing local and systemic acquired resistance systems against pathogens. Treatment with SA also modulates activities of antioxidant enzymes, thereby reducing oxidative stress and inducing crop tolerance to chilling injury. Therefore, SA can be effectively used in postharvest management of fresh horticultural produce as an alternative to harmful synthetic chemicals to enhance shelf life and ensure food safety.

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