Use of salicylic acid during cultivation of plants as a strategy to improve its metabolite profile and beneficial health effects

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REVIEW

Abstract

Chemical elicitors in plants during cultivation have been applied in soil, hydroponic solutions, or sprayed on the leaves to induce physiological changes and stimulate the production of bioactive compounds. Salicylic acid (SA) is a phenolic compound present in plants with multiple functions, including stimulus of plant growth and induction of plant defense responses under conditions of stress. Recently, the use of SA as elicitor has generated much interest, due to the growing number of studies demonstrating its positive effects in fruits, vegetables, and herbs on the induction of phytochemicals, mainly phenolic compounds, alkaloids, saponins, carotenoids, among others. The health benefits of plant materials treated with SA are mainly their antioxidant capacities determined by the 2,2'-azinobis-(3-ethylbenzothiazoline-6-sulfonic acid) (ABTS) and 2,2-diphenyl-1-picrilhidrazil (DPPH) assays and anti-inflammatory properties determined in vitro, as well as hypoglycemic and hypolipidemic properties and renal protection evaluated by in vivo studies. Therefore, the exogenous application of SA during cultivation of different plants could be an alternative to increase their economic value and could be the basis for designing standardized procedures in the production of bioactive compounds.

Keywords: antioxidant capacity; bioactive compounds; elicitation; health; salicylic acid

Introduction

Secondary metabolites of plants comprise a large group of compounds that are synthesized during their growth and do not play any role in development, photosynthesis, or reproduction. However, these compounds are crucial in several important processes, such as plant defense against environmental stresses or attack by pathogens (Cohen and Kennedy, 2010).

Plants are an important source of secondary metabolites, which have been used for the production of drugs, due to their beneficial health properties, which are associated with a protective effect against oxidative processes (Baenas *et al.*, 2014). Plants growing under unfavorable environments, such as water deficit, extreme heat or cold, oxygen deficiency, among others, result in an accelerated expression of some genes related to the synthesis of secondary metabolites. This effect has been associated with the generation of reactive oxygen species (ROS) during environmental stress (Jenks, 2007). It has been shown that similar effects can be produced intentionally during the cultivation of plants to improve their content of bioactive metabolites (Baenas *et al.*, 2014).

Optimizing the bioactive compounds' composition of plant food would be a cost-effective strategy for enhancing nutrition and preventing diseases among the population. Moreover, this approach could improve the economic value of some medicinal plants (Singh and Dwivedi, 2018). One of the most used strategies for this purpose is the exogenous application of elicitors.

Many of these compounds are naturally synthesized by plants in response to attack of pathogens (Baenas *et al*., 2014).

Among the elicitors mostly studied in recent years is salicylic acid (SA), an endogenous regulator of growth in plants that controls several physiological processes, such as systemic defense signaling against biotic and abiotic stress. Several studies have shown that exogenous application of SA also generates different changes in plant physiological processes and reactions, such as prevention of ethylene production (Khan *et al*., 2013), increase in the growth parameters (Khandaker *et al*., 2011), and modulation of the bioactive metabolite synthesis (Ananieva *et al*., 2004).

In this review, we will discuss the studies conducted in the last decades regarding the exogenous application of SA during the cultivation of plants and the effect of this treatment on bioactive metabolites of the crop. It describes the broad variety of plant secondary metabolites induced by SA, such as phenolic compounds, terpenoids, alkaloids, among others, and their health beneficial properties, which can provide an overview of the possible fields of application of the SA-elicited plant foods. Finally, we conclude our review by providing suggestions that can be applied during plant cultivation to increase the production of specific secondary metabolites.

Classification and Synthesis of Bioactive Compounds

Plant-based foods have generated great interest in research in recent years, in addition to providing macronutrients and micronutrients. These are a rich source of bioactive compounds, which, although not being classified as nutrients, or considered essential for human health, have an important beneficial impact on some diseases (Guerriero *et al*., 2018). In nature, there are three large groups of bioactive compounds, which include nitrogenous and sulfur (S) substances, terpenoid compounds, and the bioactive widely studied, the phenolic compounds (Cohen and Kennedy, 2010).

Nitrogen (N) and sulfur are the main plant nutrients and serve as constituents of proteins and several other important organic compounds that exert biological activities (such as alkaloids and glycosinolates). Furthermore, these compounds control yield and quality of plants (Ibrahim *et al*., 2012). Alkaloids are N-containing organic compounds that often contain one or more rings of carbon atoms, where nitrogen atoms are usually located and whose position of those in the carbon ring varies with different alkaloids; pyrrolidine, pyridine, quinoline, indole, steroidal, diterpenoid, and others. For some alkaloids, the nitrogen atom is not in a carbon ring (Bribi, 2018). Most alkaloids are derived from amino acids, including tryptophan, phenylalanine, lysine, tyrosine, histidine, and ornithine. Some nonamino acid compounds such as terpenoids, purine nucleotide, and polyketide are also precursors of these compounds (Ziegler and Facchini, 2007). Glucosinolates are thioglucosides with a common structure, characterized by side chain (R) with different aliphatic, aromatic, and heteroaromatic carbon skeletons, all derived from amino acids by a process of long chain elongation, hydroxylation, or oxidation (Vig *et al*., 2009).

Terpenes constitute the largest class of natural products, and these are extensively used in the industrial sector. The most important biological terpenes include carotenoids and phytosterols. Carotenoids are a group of plant pigments responsible for bright red, yellow, and orange hues in many fruits and vegetables, including alpha-carotene and beta-carotene, lutein, lycopene, β-cryptoxanthin, and zeaxanthin, among others (Singh and Sharma, 2015).

On the other hand, phenolic compounds include a large group that can be classified according to the number of phenol rings that they contain; phenolic acids, stilbenes, lignans, flavonoids (flavones, flavonols, flavanones, flavanols, anthocyanins, chalcones, dihydrochalcones, anthocyanins, and isoflavones), and tannins. Phenolic acids are constituted chemically at least by one aromatic ring, which has one hydrogen atom substituted by a hydroxyl group. These metabolites are divided in two groups: hydroxybenzoic acids and hydroxycinnamic acids (Vuolo *et al*., 2019). Stilbenes are a group of phenylpropanoid-derived compounds characterized by a 1,2-diphenylethylene backbone (C6-C2-C6). The lignans are a group of polyphenols comprising a large variety of individual structures, mostly consisting of two phenylpropanoids C6–C3 linked by a bond between the central atoms of the respective side chains (position 8 or β), also called β-β' bond (Haminiuk *et al*., 2012).

Flavonoids have a C6–C3–C6 general structural backbone in which two C6 units (Ring A and Ring B) consisting of two phenyl rings contain a heterocyclic pyrane ring (C). Due to the hydroxylation pattern and variations in the chromane ring (Ring C), flavonoids are divided into different sub-groups. Chalcones, though lacking the heterocyclic Ring C, are still categorized as members of the flavonoid family (Tsao, 2010). Flavanols or flavan-3-ols are often commonly called catechins. These compounds and epicatechin can form polymers, which are often referred to as proanthocyanidins. These are traditionally considered to be condensed tannins and the hydrolysable tannins are gallotannin or tannic acid (Haminiuk *et al*., 2012).

Regarding phenolic compounds, these are basically derived of the malonic and shikimic acid pathways, whose precursors are derived from glycolysis and the pentose phosphate pathway, resulting in the production of different compounds, such as simple flavonoids, phenolic acids, tannins, coumarins, and anthocyanins. Nitrogen-containing compounds, such as alkaloids, glucosinolates, and cyanogenic glycosides, are synthesized from amino acids like tryptophan, tyrosine, and tryptophan, also derived of the shikimic acid pathway. Terpenoids are units of isoprene, synthesized from acetyl CoA or 3-phosphoglycerate (Cohen and Kennedy, 2010) (Figure 1).

Classification of Elicitors in Plants

Secondary metabolites are ubiquitous in plants and serve different purposes; for example, they provide the blue color to blueberries and the red color to blood-oranges. They also contribute to the bitterness of grapefruits, to the astringency of unripe persimmon, and the texture of red wines (Vuolo *et al.*, 2019). During plant growth, these phytochemicals are synthesized as a defense mechanism; therefore, when plants are exposed to an adverse situation, such as pathogens attack, ultraviolet (UV) radiation, drought, heavy metals, nutrient deficiency, increased soil salinity, and other types of environmental stresses, the synthesis rate of secondary metabolites increases (Figure 2). These produce changes in the phytochemical profile after the stress situation, and these changes depend on several factors, such as the type and intensity of the stress, the plant species, and the type of metabolites involved (Kulbat, 2016).

The term elicitor originally included only molecules capable of inducing the synthesis of phytoalexins; however, nowadays, this concept is used for all compounds that induce any type of plant defense. Elicitors can be classified as biotic or abiotic, physical or chemical, and depending on their origin and molecular structure. Biotic elicitors include lipopolysaccharides, oligosaccharides, and polysaccharides, such as pectin and cellulose, chitosan, chitin and glucans, galacturonides, some proteins including cellulase, cryptogein, glycoproteins, oligandrin and pectolyase, as well as other compounds of complex composition, such as fungal spores, mycelia cell wall, and microbial cell wall. On the other hand, abiotic elicitors can be chemicals, for example, acetic acid, benzothiadiazole, silicon, ethanol, ethene, hydrogen peroxide, inorganic salts, and metal ions or physical as an altered gas composition, chilling, CO2, drought, extreme temperatures, high pressure, high or low osmolarity, UV irradiation, saline stress, wounding and ozone, among others. Furthermore, some plant hormones acts as elicitors, either when they are produced by the plant in response to some pathogen attack or when they are applied exogenously in low concentrations to the plants during cultivation. Examples of these compounds are jasmonic acid, methyl jasmonate, ethylene, cytokinin, gibberellin GA3 methyl salicylate, and SA (Baenas *et al.*, 2014).

Salicylic Acid

SA is a phenolic compound, consisting of a ring linked to a hydroxyl and a carboxyl group. This acid regulates physiological functions in plants, when it is exogenously

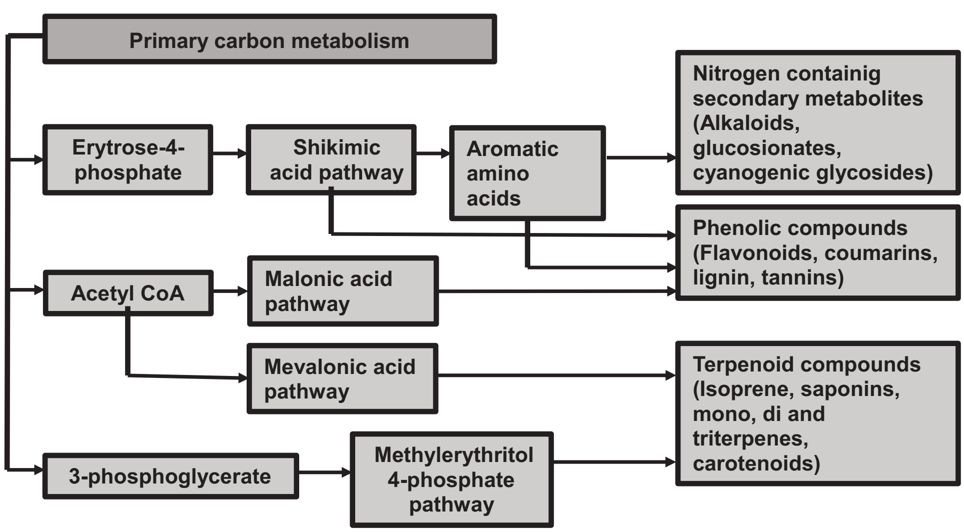

Figure 1. General outline of biosynthetic pathways of secondary metabolites in plants.

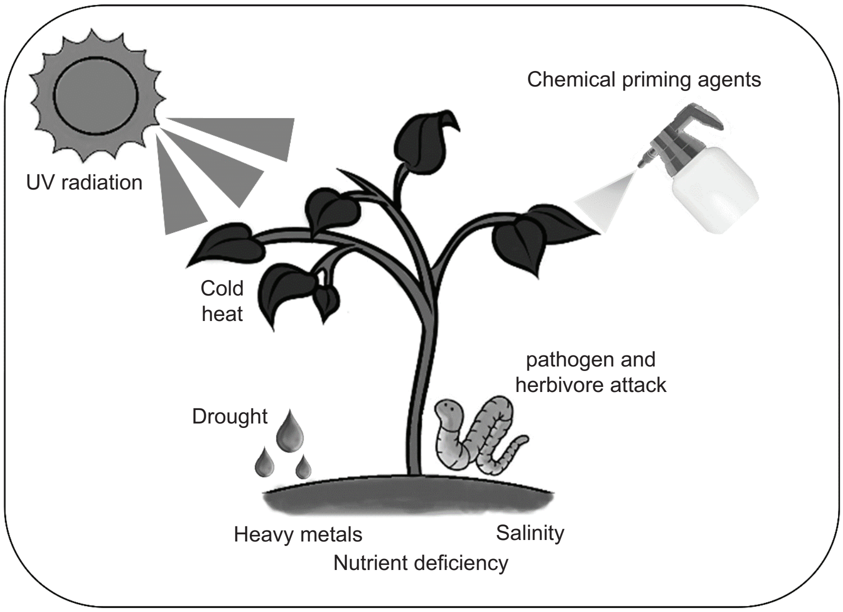

Figure 2. Production of bioactive metabolites in plants under environmental stress factors.

applied, plays an important role in the germination of seeds, either by inhibiting germination or increasing seed vigor, depending on the concentration. Recent studies also suggest that SA is a regulator of photosynthesis, it controls chloroplast and leaf structure, stomatal closure, chlorophyll and carotenoid accumulation, and the activity of important enzymes related to photosynthesis, such as RuBisCO (ribulose-1,5-bisphosphate carboxylase/oxygenase) and carbonic anhydrase. In addition, SA participates in the regulation of the alternative oxidase (AOX) route both in thermogenic and nonthermogenic plants through the induction of gene expression. AOX combines ubiquinol oxidation with the reduction of molecular oxygen to produce water in a reaction that is not sensible to inhibitors of the cytochrome oxidase pathway, which allows the control of ATP synthesis to keep the homeostasis and regulate the growth of plants. These growth-promoting effects of SA in plants are also related to the increase in photosynthesis, to changes in the hormonal status, transpiration, and stomatal conductance (Lefevere *et al*., 2020).

Other studies have demonstrated that SA is involved in the regulation of flowering by interacting with components of the photoperiod pathway through a CO-independent branch. SA is also involved in the regulation of senescence, which is characterized by a decrease in the photosynthetic activity, a loss of antioxidant capacity, and therefore higher levels of ROS (Dempsey *et al*., 2011).

SA is widely distributed in plants at different basal levels depending on plant species. SA is synthesized by two different compartmentalized routes with different precursors: in the cytoplasm starting from phenylalanine by the phenylpropanoid pathway and in the chloroplast through the isochorismate pathway (Gondor *et al*., 2016) (Figure 3). Phenylalanine ammonia-lyase (PAL) is the enzyme that initiates the phenylpropanoid pathway by transforming phenylalanine into trans-cinnamic acid and NH3 through a nonoxidative deamination. Trans-cinnamic acid participates as a precursor of diverse phenolic compounds biosynthesis, such as lignin, lignans, and flavonoids. Furthermore, some studies indicate that SA is also synthesized from phenylalanine, via trans-cinnamic acid, which is then converted into SA via two intermediates: ortho coumaric acid or benzoic acid, depending on the plant species (Dempsey *et al*., 2011). Plants can use three biosynthetic routes to produce benzoic acid: a β-oxidative and a nonoxidative route from cinnamoyl Co-A and a nonoxidative route from trans-cinnamic acid (Zhang *et al*., 2014).

Regarding the isochorismate pathway, it is known that chorismate is synthesized in the plastid, and is then converted into isochorismate by an isochorismate synthase (ICS). After that, an amino acid conjugation of isochorismate, followed by a enzymatic conversion or a spontaneous decomposition results in the synthesis of SA and the gene responsible for this conversion is PBS3 (Lefevere *et al*., 2020).

Due to the importance of both PAL and ICS in SA accumulation, it is possible that the PAL and ICS routes are integrated by a metabolic or regulatory grid in the biosynthesis of this hormone. The recently identified genes PBS3 and EPS1 have demonstrated to be important in

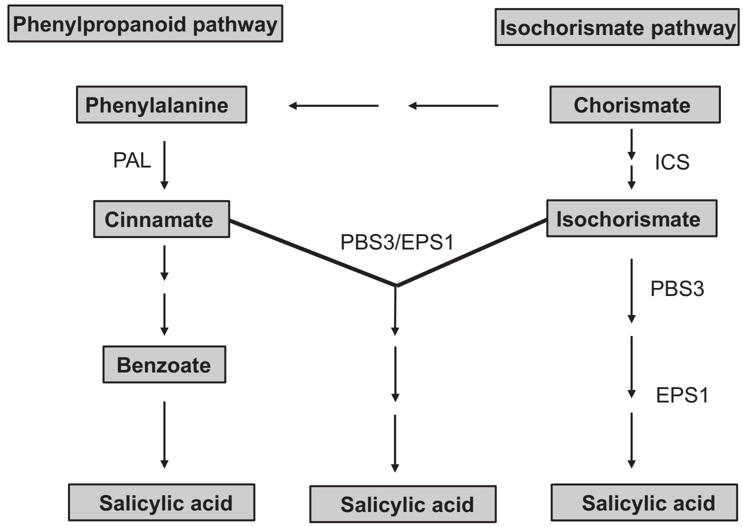

Figure 3. Biosynthesis of SA in plants. PAL: Phenylalanine ammonia-lyase; PBS3: Proteasome subunit beta type-3; EPS1: ER-retained Pma1 Suppressing; ICS: Isochorismate synthase.

the pathogen-induced SA production and to encode enzymes that catalyze reactions involved in the synthesis of SA (Dempsey *et al.*, 2011).

Pathtways Induced by SA as Elicitor

SA has been intensively studied in recent years due to its function as an endogenous signal mediating local and systemic plant defense responses against pathogens (Aftab *et al.*, 2010). In addition, it has also been demonstrated that SA is involved in the plant response to different types of abiotic stresses such as drought, chilling, heavy metal toxicity, heat, and osmotic stress, playing a crucial role in the regulation of physiological and biochemical processes in plants (Vicente and Plasencia, 2011). It has been demonstrated in different plant species that exogenous application of SA induces synthesis and accumulation of antioxidant compounds. The molecular mechanism of elicitation by SA is complex and depends on the concentration applied, the growth stage and nutritional uptake by plants, environmental conditions, etc. SA regulates the PAL enzyme activity, which catalyzes key biosynthetic reactions to produce secondary metabolites that act as a defense mechanism against environmental stresses (Puthusseri *et al.*, 2012).

Signal recognition of SA is mediated by receptors and binding sites located on the plasma membrane, such as NPR1, NPR3, and NPR4, which activate a complex cascade of events that is initiated by inhibiting the activity of catalase, the enzyme responsible for breaking down hydrogen peroxide in water and oxygen. This produces an increase in the H_2O_2 levels, which produces an elevation in OH radicals that generate an oxidative stress status in cells, which in turn initiates a series of signaling cascades that involve the activation of Mitogen-Activated Protein Kinases (MAPKs) and G proteins, which leads to an increase in the production of secondary metabolites (Khalil *et al.*, 2018). Calcium flux also participates as signaling in plant cells after SA exogen application (Rodas-Junco *et al.*, 2013). In unstimulated cells, Ca_{2+} concentrations in cytosol are maintained at lower levels; when plants are attacked by a pathogen, their abscisic acid levels increase in response to the attack, which activates calcium channels, causing a Ca_{2+} influx into cytosol. It is known that exogenous SA also produces an increase in abscisic acid levels in the plant, which causes the same effect as a pathogen attack, increasing the calcium concentrations in the cytosol. This Ca_{2+} influx is involved in diverse physiological and cellular processes, associated with Ca_{2+}-binding proteins, calcium-dependent kinases (CDPKs), phospholipases, and through secondary messengers such as inositol 1,4,5- triphosphate (IP3) and diacylglycerol (DAG). CDPKs trigger diverse signaling cascades to coordinate cellular processes such as regulation of the oxidative stress, hormonal signaling, and gene expression (Herrera-Vásquez *et al.*, 2015). Furthermore, studies have shown that G-proteins play an important role in stimulating ion channels, phospholipases A, C, and D, ROS generation, and apoptosis. $_{G-}$protein activation stimulates the accumulation of cAMP, IP_3 and DAG, which triggers the activation of PKA and PKC. This causes the phosphorylation of MAPKs, resulting in gene expression that leads to several enzymatic reactions involved in secondary metabolite production (Rodas-Junco *et al.*, 2015; Ruelland *et al.*, 2014) (Figure 4).

SA and Bioactive Compounds

There are a large number of studies that demonstrate the beneficial health properties of secondary metabolites in plants, which vary depending on the compound's structure and concentration. It has been reported that some nitrogen compounds, such as alkaloids, among which are choline, trigonelline, sitsirikine, and others, exert several pharmacological effects, including anti-inflammatory, anti-diarrheal, anti-cancer activities, and therapeutic potential for hypertension, hyperlipemia, diabetes, cardiovascular system, and central nervous system diseases (Qian *et al.*, 2017). Sulfur substances predominate in some vegetables of the cabbage family, onions, garlic, etc. Garlic and onion contain sulfur compounds, such as allicin (2-propene1-thiolsulfinate), thiosulfinates, diallyl disulfide, and S-alk(en)yl-L-cysteine sulfoxides, which have been associated with health properties such as antioxidants, antibacterial, anti-inflammatories, and inhibitors of the proliferation of human tumor cells (Higuchi *et al.*, 2003).

Many terpenoids have biological activities, particularly against certain cancers and eye disease (Johnson, 2002). On the other hand, phytosterols, mainly sitosterol, stigmasterol, and campesterol, are associated with the reduction of risk of coronary heart disease by improving LDL cholesterol concentrations. They also have anti-cancerous properties and are immune system modulators (Chawla and Goel, 2014).

Phenolic compounds have shown various beneficial effects on human health, such as anti-aging, anti-inflammatory, antioxidant, and anti-proliferative activities. So they have been pointed out as an alternative to improve the incidence of certain chronic diseases, such as diabetes, cancer, and cardiovascular diseases, through the control of oxidative stress (Lin *et al.*, 2016).

There are an increasing number of studies that evaluate the exogenous application of SA to different plant species and the effects on its content of bioactive compounds (Table 1). The foliar application of SA has increased the total phenolic compounds and total flavonoids on *Solanum lycopersicum* (Javanmardi and Akbari, 2016), *Amaranthus tricolor* L (Khandaker *et al.*, 2011), *Ocimum basilicum* (Gharib, 2007), *Achillea millefolium* (Gorni and Pacheco, 2016), and *Mentha pipperita* (Figueroa-Perez *et al.*, 2014, 2015, 2018).

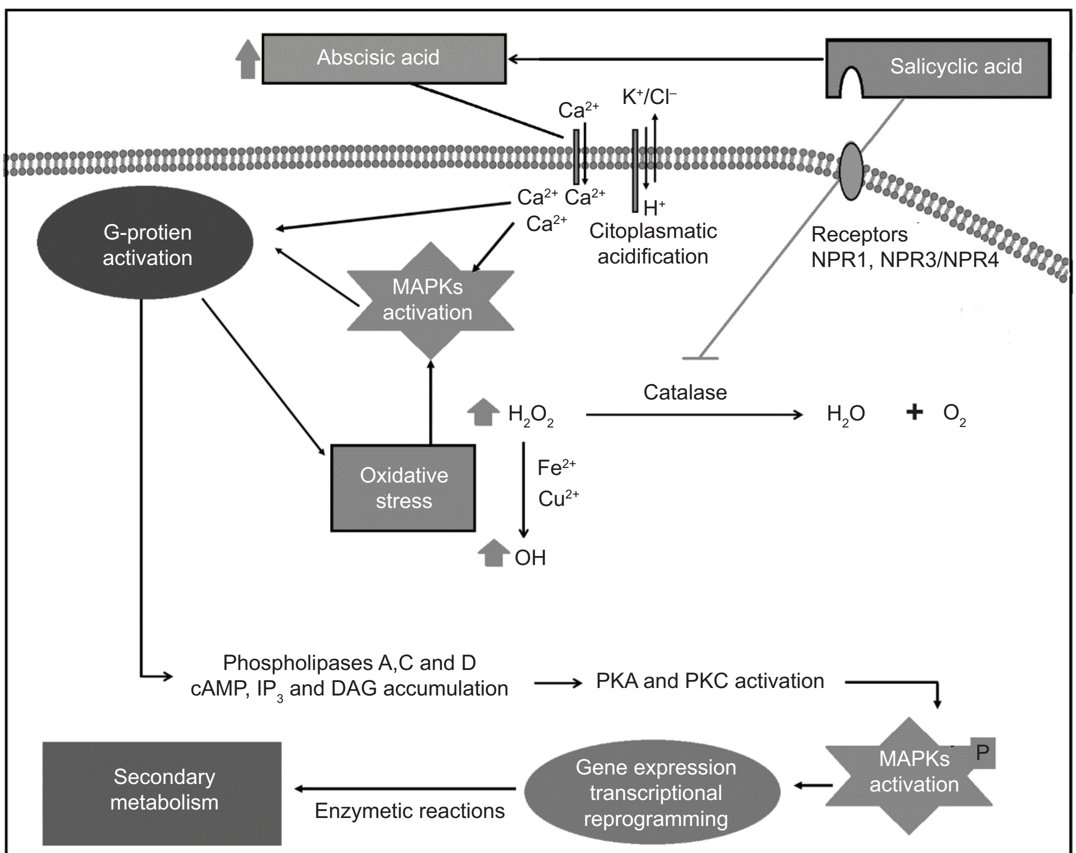

Figure 4. General mechanism induced by elicitation with SA. MAPKs: Mitogen-Activated Protein Kinases, cAMP: Cyclic adenosine monophosphate, IP_3: Inositol 1,4,5-triphosphate, DAG: Diacylglycerol, and PKA and PKC: Protein kinase A and C.

On the other hand, it has been shown that SA elicitation could improve other bioactive compounds. For example, saponins and alkaloids have been detected in *Mentha pipperita* (Figueroa-Pérez *et al.*, 2018). Isatis tinctoria L. hairy root cultures treated with SA increased the alkaloid content (Qing-Yan *et al.*, 2019). SA applied to root cultures of Stemona curtisii significantly improved the production of the alkaloids, namely, oxyprotostemonine, stemocurtisine, and stemocurtisinol (Chotikadachanarong *et al.*, 2011).

It has been found that foliar application of 2 mM SA in peppermint plants increased their phytosterols contents, such scholine, trigonelline and vinblastine (Figueroa-Perez *et al.*, 2015). Carotenoid content, mainly crocin, was highly improved in *Crocus sativus* plants after SA application (Tajik *et al.*, 2015). Likewise, foliar application of SA in yarrow (*Achillea millefolium* L.) plants resulted in linear increases in chlorophyll content, as well as a high production of essential oils. Furthermore, addition of SA to the medium of *Alternanthera tenella* leaves cultured *in vitro* induced an increase in betacyanins of the leaves (Gorni and Pacheco, 2016).

The molecular response mechanism underlying SA elicitation involves the upregulation of some genes related to the alkaloids and flavonoids synthesis, such as aromatic amino acid decarboxylase (AADC), YUCCA monooxygenase (YUCCA), 4-coumarate coenzyme A ligase (4CL), chalcone synthase (CHS), chalcone isomerase (CHI), and flavonoid 3′-hydroxylase (F3′H). Specifically, YUCCA gene exhibits the greatest transcriptional abundance for the maximal alkaloid production in Isatis tinctoria L. hairy root cultures after SA elicitation, which suggested that this gene might be more sensitive and key for inducing alkaloid biosynthesis (Qing-Yan *et al.*, 2019).

Health Benefits of licited Plants with SA

There are several studies on the effect of elicitation with SA on the metabolite content of plants. The main effects with health benefits determined in these plants have been related to their antioxidant capacities.

It has been shown that the application of salicylic acid 1 mM during cultivation of Saffron (*Crocus sativus* L.) increased the crocin content (a carotenoid responsible for the color of flowers) and improves the antioxidant activity of stigmas.(Tajik *et al.*, 2015). Furthermore, elicitation with 300 μM SA in plant cell suspension cultures of *Thevetia peruviana* increased the antioxidant capacity by 1.66-fold determined by the ABTS assay, compared to the control culture (Mendoza *et al.*, 2018).

Blanch *et al.* (2020) found that foliar application of SA (100 mg/L) during cultivation of *Vitis vinifera* cv Syrah plants, significantly increased (3-fold) the antioxidant capacity of the fruits, this effect was associated to increases of some phenolic compounds, such as myricetin, trans-resveratrol and phenolic acids, mainlygallic, chlorogenic, caffeic and trans-ferulic acids.

Furthermore, it has been shown that 12 mM SA applied postharvest to Kinnow mandarin under cold storage increased twofold the total antioxidant capacity of the fruits determined by DPPH test. SA treatment also improved the activity of the antioxidant enzymes catalase, peroxidase, and superoxide dismutase. These enzymes help to scavenge free radicals in the fruit, which can damage the cells under stress. These effects were related to phenolic compounds and ascorbic acid content (Haider *et al.*, 2020).

Lee *et al.* (2013) showed that SA-treated *Aloe vera* adventitious roots cultured on MS liquid media decreased the anti-inflammatory activity in UVB-treated mouse skin cells, suppressing the activity of COX-2, NF-kB, and AP-1. Foliar spraying of 2 mM SA in *Ammi visnaga* potentiated the radical scavenging activity of plant extracts using DPPH assay and these effects were higher for drought stressed aerial parts sprayed with 2 mM SA. The cytotoxic activity of extracts of *Ammi visnaga* were evaluated against different cell lines as liver cancer (HepG2), breast cancer (MCF-7), lung cancer (A549), and colon cancer (Caco2), and the major effect was observed for the methanolic extracts of the fruits, roots, aerial parts, and umbels against MCF7 cell line and fruits for HepG2 cell line (Osama, 2019). It also has been reported that application of 2 mM SA during 60 min to *Centella asiatica* (L.) leaves effectively inhibited nitric oxide (NO) production in LPS-stimulated RAW 264.7 macrophage cells, related to the reduction in the transcription level expression of iNOS in a dose-dependent manner, which suggests that elicitation with SA increased anti-inflammatory activity in *Centella asiatica* leaves (Buraphaka and Putalun, 2020). On the other hand, it has been demonstrated that the administration of infusion prepared with 2 mM SA-treated peppermint to diabetic rats for 4 weeks, decreased serum glucose (up to 25%) and increased serum insulin levels (up to 75%) as compared to diabetic controls. Furthermore, these infusions prevented oxidative damage on pancreas β-cells, improved serum lipid profile, and decreased hepatic damage in diabetic rats (Figueroa-Perez *et al.*, 2015). Also, they decreased the renal accumulation of 14 inflammation-related proteins, associated with glomerular hypertrophy, tubular damage, expansion of mesangial matrix, and cell death in diabetic rats (Figueroa-Pérez *et al.*, 2018). In addition, it has been

Table 1. Bioactive metabolites' content of food plants in response to the application of salicylic acid during its cultivation.

No.	Plant species	Dose and mode of application of SA	Target compounds and increase	Reference
1	Tomato (*Solanum lycopersicum*)	Foliar application at 450 mg/L, 3 weeks after fruiting under greenhouse conditions	Total phenolic compounds (2.1-fold); total flavonoids (1.2-fold); vitamin C (2.8-fold)	(Javanmardi and Akbari, 2016)
2	Chinese chive (*Allium tuberosum*)	Foliar application of 500 and 150 μM SA	Chlorophyll, phenols and flavonoids, vitamin C, and volatile components	(Wang *et al*., 2022)
3	(*Coriandrum Sativum*)	Supplementation with 225 mg/L SA on the growth medium during 30 days	Gallic, benzoic, ferulic and 3-O- Caffeoylquinic acids, Querecetin-3-O-rutinooside, and glucronide and kaempferol-3-O-rutinoside	(Kdhim *et al*., 2020)
4	Red amaranth (*Amaranthus tricolor* L.)	Foliar application at 10^{-5} M under greenhouse conditions 1 week after sowing	Total phenolic compounds (1.2-fold); betacyanins (1.3-fold); chlorophyll (1.3-fold)	(Khandaker *et al*., 2011)
5	Sweet basil (*Ocimum basilicum* L.)	Foliar application at 1 mM to 1-month old plants under controlled environmental conditions	Total flavonoids (1.9-fold); total phenolic compounds (1.3-fold); total flavanols (1.7-fold)	(Karalija and Parić, 2017)
6	Peppermint (*Mentha piperita*)	Foliar application at 0.5 and 2 mM, two doses 45 and 60 days after planting	Rosmarinic acid (1.7-fold); hesperidin (1.5-fold); gallatocatechin-gallate (2.8-fold); quercetin (1.6-fold); serjanic acid 3β-arabinopyranoside (9-fold); stigmasteryl 3β-D-glucopyranoside (2-fold); trigonelline (1.8-fold)	(Figueroa Perez *et al*., 2014, 2015)
7	Broccoli (*Brassica oleraceae*)	Daily exogenous spraying at 100 μM to 7-day-old sprouts on days 3, 5 and 7	Indole glucosinolate (1.3-fold)	(Pérez-Balibrea *et al*., 2011)
8	Yarrow (*Achillea millefolium*)	Foliar application at 0.5 mM 20 days after transplanting the seedlings	Chlorophyll (1.6-fold); essential oils (2-fold); total phenolic compounds (1.5-fold)	(Gorni and Pacheco, 2016)
9	Chamomile (*Matricaria chamomilla*)	Foliar application at 7 mM on 6-week-old plants in stage of leaf rosette	Herniarin (2.4-fold); Z)- and (E)-2-β-d-glucopyranosyloxy-4-methoxycinnamic (1.8-fold)	(Dučaiová *et al*., 2013)
10	St John's-wort (Hypericum perforatum)	Foliar application at 2 mM in a single dose and harvested 7 days later	Total phenolic compounds (1.9-fold); uliginosin B (1.6-fold)	(de Matos Nunes *et al*., 2014)
11	Marjoram (*Origanum majorana*)	Foliar application at 1 mM on 2-month- old plants, at two doses: after 75 days after sowing and 1 week later	Chlorophyll (1.4-fold); proline (1.6-fold); microelements content (1.2-2-fold)	(Gharib *et al*., 2007)
12	Ginger (*Zingiber officinale Roscoe*)	Foliar application at 1 mM at the second leaf stage once a week for 4 weeks	Myricetin (2-fold); fisetin (2-fold); morien (1.6-fold); anthocyanin (2-fold)	(Ghasemzadeh *et al*., 2012)
13	Scarlet sage (*Salvia coccinea*)	Foliar application at 1 mM SA three times, every 7 days to plants growing under salt stress conditions	Total phenolic compounds (1.2-fold); total carotenoids (1.4-fold)	(Grzeszczuk *et al*., 2018)
14	Thyme (*Thymus vulgaris*)	Foliar application at 3 mM every 21 days for 2 months to 1-month-old plants	Total flavonoids (2-fold); total phenolic compounds (2-fold); kaempferol-3-glucoside (2-fold); apigenin 7-O-glucuronide (2-fold); chlorogenic acid (1.6-fold); rosmarinic acid (1.3-fold); eriocitrin (2-fold); dihydroquercetin (2.3-fold)	(Khalil *et al*., 2018)
15	Sweet wormwood (Artemisia annua L.)	Twenty-one-day-old plants growing in a hydroponic solution supplemented with 100 μM SA for 5 days	Carotenoids (1.2-fold); artemisinin (14-fold); dihydro artemisinic acid (5-fold)	(Kumari *et al*., 2018)
16	Aloe vera (Asphodeloideae)	Thirty-five-day-old adventitious roots growing in a hydroponic solution supplemented with 2 mM SA for 7 days	Aloe emodin (11-fold); chrysophanol (13-fold)	(Lee *et al*., 2013)

(*continues*)

Table 1. Continued.

No.	Plant species	Dose and mode of application of SA	Target compounds and increase	Reference
17	Canola (*Brassica napus* L.)	One-week-old seedlings growing in nutrient solution supplemented with 5 µM SA	Chlorophyll a (2-fold)	(Monireh *et al.*, 2011)
18	Quinoa (*Chenopodium quinoa*)	Foliar application at 400 mg/L during vegetative growth at 45 and 60 days after sowing	Chlorophyll a (1.5-fold) and b (2.5-fold); total carotenoids (2.4-fold); total phenolic compounds (1.5-fold)	(Abd Allah *et al.*, 2015)
19	Artemisinin (*Artemisia annua* L)	Foliar application at 1 mM at 10-day intervals starting from 30 days after planting and ending at day 90	Artemisinin (1.5-fold); total chlorophylls (1.3-fold); total carotenoids (1.2-fold)	(Aftab *et al.*, 2010)
20	Wheat (*Triticum aestivum*)	0.5 mM SA was added to the hydroponic solution of 2-week-old plants and collected 7 days later	Quercetin (9-fold); myricetin (4.8-fold); rutin (1.9-fold)	(Gondor *et al.*, 2016)
21	Bergamot (*Monarda didyma*)	Foliar application of salicylic acid at a concentration of 1 mM	Hydroxycinnamic acids, flavonoids, and phenolic compounds	(Skrypnik *et al.*, 2022)
22	Centella asiatica (L.)	2 mM SA was added to leaves for 40 min	Triterpenoids around 1-3-fold (Asiatic acid, madecassic acid, asiaticoside, and madecassoside)	(Buraphaka and Putalun, 2020)
23	Aloe vera (Asphodeloideae)	4 mM SA was added to the nutritive solution of 3-week-old plants and collected 14 days later	Aloe emodin (5.6-fold); chrysophanol (12-fold)	(Lee *et al.*, 2013)
24	Niagara Rosada (*Vitis labrusca*) grape	Foliar application of 1 and 2 mmol L−1 SA in the preharvest period	Rutin, cyanidin-3,5-diglucoside and 3-O-glycosidic delphinidin	(Gomes *et al.*, 2021)
25	Flame grapes (*Vitis vinifera*)	Six applications of 0.25, 1, and 2 mM of SA in the veraison stage.	Phenolic compounds, anthocyanins, and flavonoids	(Vazquez *et al.*, 2022)

shown that hypolipidemic properties of common beans sprouts can be significantly improved by elicitation with 1 and 2 mM SA, which decreased TAG intestinal absorption in rats fed with a high fat and fructose (HFF) diet and supplemented with bean sprouts (10%), this beneficial effect was associated to an increase in hesperidin and soysaponin-I contents of elicited sprouts (Mendoza-Sanchez *et al.*, 2019).

Future Trends

Research oriented to the production of functional foods has been growing over the last years due to the increasing interest of people to consume natural products. Bioactive metabolites extracted from medicinal plants have a great therapeutic value for which they are used all over the world. The food industry continues to look for ingredients with nutritional and nutraceutical properties, to develop functional products with elevated health beneficial properties (Singh and Dwivedi, 2018). However, in many cases, the cultivation conditions of the raw material used to produce nutraceutical foods are not controlled, which generate variations in its bioactive metabolite content, and therefore, its health beneficial properties. Furthermore, in some cases, the plant has a low potential for chemical synthesis of these compounds; thus, it is important to establish a regulation of natural products used in the food industry and generate strategies to produce quality nutraceutical foods (Baenas *et al.*, 2014).

SA as an elicitor may be a complementary tool to breeding programs, production management, or genetic engineering applications. The controlled short-time elicitation with SA at low doses, during the cultivation of some medicinal plants, can be used by the producers to obtain healthier products with enhanced bioactive metabolites content. Also, these preharvest treatments with SA can be of great interest for the pharmaceutical industry as tools to enhance the extractable yields of specific active compounds in plants with medicinal properties. Understanding how a plant changes its content of bioactive metabolites in response to a specific SA treatment would increase the economic value of medicinal plants and could be the basis for designing standardized procedures that generate high-quality nutraceutical foods.

On the other hand, it would be of great interest for the evaluation of nutraceutical properties of SA-elicited plants, including biological studies, to demonstrate the potential to produce safe and valuable nonpharmacological alternatives for human health through this strategy, which may provide a new approach for disease prevention and treatment.

Conclusion

The controlled use of elicitors of SA as preharvest treatment of some medicinal plants could be an effective strategy to obtain tailored foods with enhanced health-promoting compounds. Exogenous application of SA to fruits, vegetables, and herbs during cultivation produces significant increases in the content of bioactive metabolites, such as phenolic compounds, alkaloids, saponins, vitamins, carotenoids, among others. These changes in the plant could improve its health beneficial properties, such as antioxidant, antidiabetic, anticancer, and antiobesogenic, among others. However, since the effects of these elicitors depend on many factors, including the plant species, it is important to conduct studies oriented to elucidate the specific effect of SA on the plant of interest, to establish protocols that result in the controlled production of bioactive compounds.

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