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Review

Elicitors: A Tool for Improving Fruit Phenolic Content

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Abstract: Fruits are one of the most important sources of polyphenols for humans, whether they are consumed fresh or as processed products. To improve the phenolic content of fruits, a novel field of interest is based on results obtained using elicitors, agrochemicals which were primarily designed to improve resistance to plant pathogens. Although elicitors do not kill pathogens, they trigger plant defense mechanisms, one of which is to increase the levels of phenolic compounds. Therefore, their application not only allows us to control plant disease but also to increase the phenolic content of plant foodstuffs. Pre- or post-harvest application of the most commonly used elicitors to several fruits is discussed in this review.

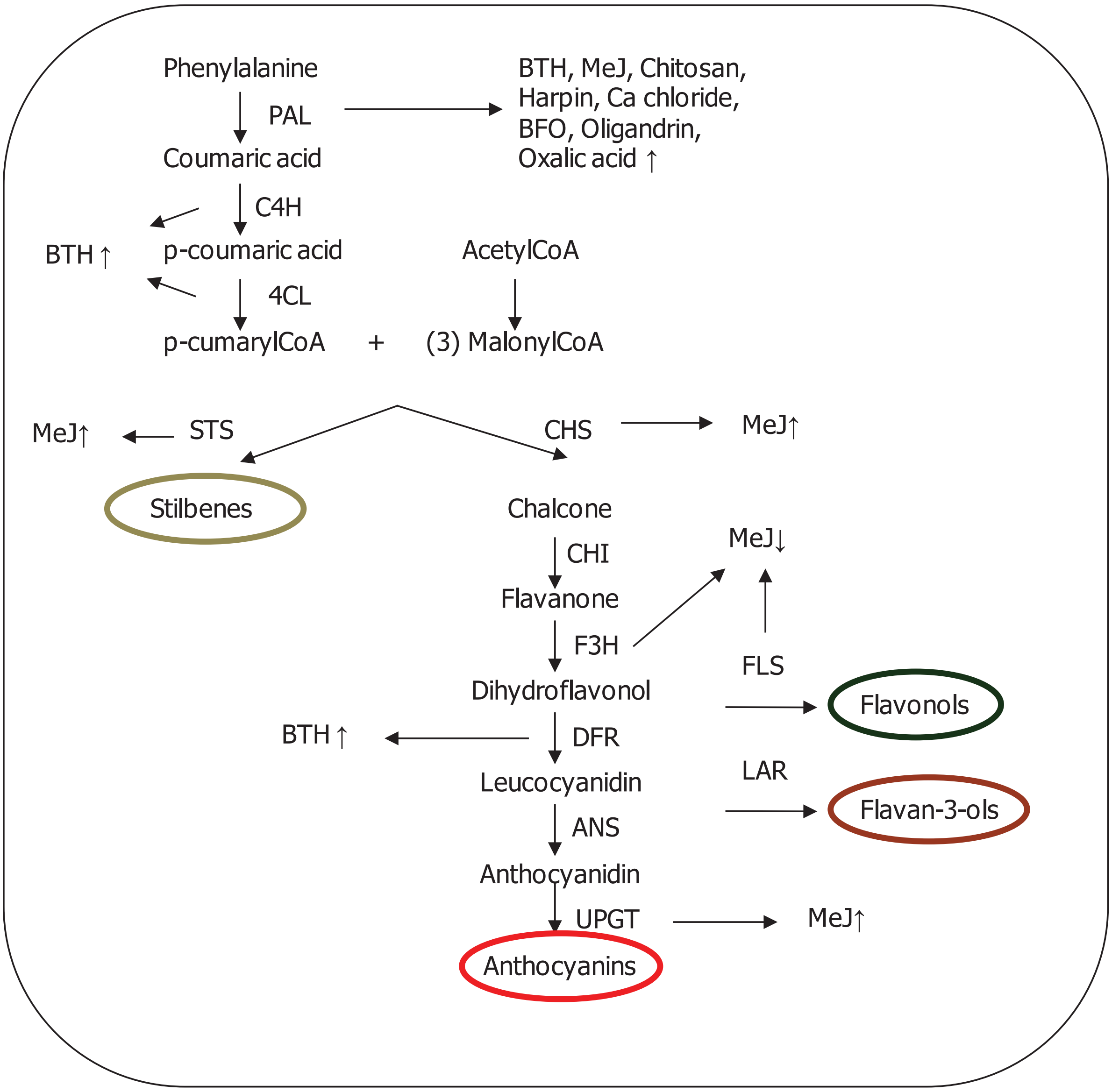
Keywords: elicitor; benzothiadiazole; methyl jasmonate; chitosan; harpin; salicylic acid

1. The Importance of Plant Phenolic Compounds

Fruits, consumed fresh or as processed products, are among the most important sources of polyphenols for humans. These compounds are secondary metabolites with various chemical structures, although a benzene ring with one or more hydroxyl groups is a common feature. They are usually classified as flavonoids (anthocyanins, flavonols, flavan-3-ols, proanthocyanidins or non- hydrolyzable tannins, flavones, isoflavones, and flavanones) and non-flavonoids (hydroxycinnamic acids, hydrolyzable tannins, hydroxybenzoic acids and stilbenes) [1].

Polyphenols are synthesized from the phenylalanine produced by the shikimic acid pathway (see Figure 1). The deamination of phenylalanine catalyzed by enzyme phenylalanine ammonia-lyase (PAL) is the first step in this biosynthetic pathway. Two of the most important classes of compound, flavonoids and stilbenes, are produced through a bifurcation of this pathway. The enzymes chalcone synthase (CHS) and stilbene synthase (STS) convert the phenylpropanoid structure cumarylCoA into a polyphenol through the formation of an aromatic ring, involving the addition of three more units of C2 (consisting of two C atoms).

Figure 1. Summary of polyphenol synthesis and enzyme regulation by elicitors.



Abbreviations: 4-CL: 4-coumarate/coenzyme A ligase; ANS: anthocyanidin synthase; C4H: cinnamate 4-hydroxylase; CHI: chalcone isomerase; CHS: chalcone synthase; DFR: dihydroflavonol 4-reductase; F3′H: flavonoid 3′-hydroxylase; F3′5′H: flavonoid 3′,5′-hydroxylase; FLS: flavonol synthase; LAR: leucoanthocyanidin reductase; PAL: phenylalanine ammonia-lyase; STS: stilbene synthase; UPGT: UDPglucose, flavonoid-*O*-transferase (UPGT); BTH: benzothiadiazole; MeJ: methyl jasmonate; BFO: Burdock fructooligosaccharide; ↑: increase in enzyme activity; ↓: decrease in enzyme activity.

Polyphenolic compounds are important for both plants and humans for several reasons. Firstly, they protect plants from biotic and abiotic stress factors. Indeed, some of these phenolic compounds are only induced when stress factors are present, among them, the so-called phytoalexins, which are specifically involved in defense mechanisms and are synthesized after pathogen or predator attack or injury [2]. Secondly, most of these metabolites are responsible for the organoleptic and qualitative properties of foods originating from such plants. For example, anthocyanins, constitute a pigment group responsible for the color of a great variety of fruits, flowers and leaves [3], and flavan-3-ols are polyphenols involved in the bitterness and astringency of tea, grapes and wine [4,5]. Thirdly, these compounds are unique sources of industrial material in the form of food additives, pharmaceuticals and flavors [6]. Finally, they are considered to be beneficial for health, mainly due to their antioxidant activity. Many studies have suggested that a high intake of polyphenol-rich foods may have cardiovascular benefits, and provide some level of cancer chemopreventive activities and beneficial effects against other less prevalent but devastating illnesses, such as Alzheimer's disease and urinary bladder dysfunctions [7–10]. Phenols act as antioxidants through different mechanisms [11]: (1) hydroxyl groups with π electrons of the phenyl can capture free radicals; (2) the generation of free radicals catalyzed by metals is diminished since they chelate metallic ions; (3) the cycle of generating new radicals is stopped through the donation of a proton from the phenolic compounds to the radicals and (4) polyphenols inhibit pro-oxidant enzymes that generate free radicals, such as lipoxygenases, cyclo-oxygenases and xanthine oxidase.

2. Methods for Improving Plant Phenolic Content

For all the above reasons, different methods to improve the polyphenol content of plants have been developed. The most common techniques affect cultural practices such as pruning, cluster thinning or the use of deficit irrigation. Perez-Lamela *et al.* [12] studied the influence of the training system and pruning of three varieties of red grape (*Vitis vinifera* L.) on the color intensity, total polyphenol content, total anthocyanins and tannins in wine made from them. The effect of pruning intensity on total phenolics was also investigated in mangoes. Moderate pruning significantly increased total phenolics, while the lowest contents were recorded in non-pruned trees [13]. Cluster thinning was found to increase the total anthocyanin concentration and pruning the total anthocyanin potential in Tannat and Malbec red grapes [14,15]. Soufleros *et al.* [16] also found that cluster thinning increased total anthocyanins and skin tannin content of red grape during ripening from 52% to 89% and from 56.2% to 114%, respectively, depending on the plot studied.

Another cultural practice that may modify the plant phenolic content is deficit irrigation. When applied pre-veraison, it caused an increase in skin anthocyanin concentration in Cabernet Sauvignon grapes [17]. Basile *et al.* [18] studied different irrigation regimes at three development stages of the grapevine, finding that the concentration of anthocyanins and polyphenols was improved when no water stress occurred from anthesis to fruit set, followed by mild water stress between fruit set and veraison and moderate to severe water stress post-veraison. Similar results were found by Romero *et al.* [19], also in grapevine. When regulated deficit irrigation strategies were applied to olive trees during fruit ripening and at different harvesting times to study the effect on oil yield and oil composition, the polyphenol content and stability of oils increased on all picking dates, especially during the first stages of the ripening period [20].

Classical breeding methods to improve certain characteristics in plants have been practiced for many years. Plant breeding can be accomplished by different techniques like simply selecting plants with desirable characteristics for vegetative propagation, the deliberate crossing of closely or distantly related individuals to produce new crop varieties or lines (called hybrids) with desirable properties, and selecting clones from the same variety that express interesting attributes. Genetic factors within crop populations may have important effects on the phenolic content, most observed changes usually being quantitative rather than qualitative [11]. In this way, the anthocyanin profile and color characteristic of a collection of 143 plants arising from crosses from Monastrell × Cabernet Sauvignon grapes was studied to select plants showing the most interesting enological characteristics. As a result, seedlings with a very interesting phenolic profile were identified, due to their composition and concentration [21]. The grape skin and seed proanthocyanidin profiles from Monastrell × Syrah grape (*Vitis vinifera* L.) crosses were determined by Hernandez-Jimenez *et al.* [22], who found that the proanthocyanidin composition of crosses was qualitatively similar to that of Monastrell and Syrah, but, quantitatively, grapes with very high procyanidin content were observed. Crosses of other types of fruit have also been performed in order to improve their polyphenolic content. For instance, in citrus, Tusa *et al.* [23] found ten flavonoids and four hydroxycinnamic acids in all hybrids of orange x lemon analyzed, one of the hybrids showing an intermediate polyphenol composition with respect to that of the parents. The quality of the juices from mandarin-like hybrids was studied to identify plants with high content of polyphenols [24]. Also, the content of ascorbic acid, total phenolics, flavanones, anthocyanins and phenolic acids were investigated in orange hybrids and their juices. The so called OTA 9 hybrid was found to be the richest in polyphenols [25]. Other examples include hybrids of different berries such as blackberries, raspberries, red currants, gooseberries and cornelian cherries that were assayed for antioxidant activity, ascorbic acid, phenol, and anthocyanin contents. In the above study, Pantelidis *et al.* [26] found that the anthocyanin and phenol contents varied widely, depending on the particular hybrid. Bugaud *et al.* [27] studied the total polyphenol content of bananas, finding that the total polyphenol contents of the hybrids were three-fold higher than bananas of the Cavendish variety.

Clone selection is also an important tool for improving fruit traits such as their phenolic content. In a study of different clones of Tempranillo grapes, Revilla *et al.* [28] observed differences in their phenolic content. The phenolic composition of clones from a given variety may be so different that can be used as discriminant factor among the clones. For example, anthocyanins, flavonols and hydorxycinnamic acids were used to discriminate between *Vitis vinifera* L. cv. "Barbera" clones [29]. In addition, some clones have been shown to have the capacity to produce wines with a distinct color, chromatic profile and phenolic content [30]. Burin *et al.* [31] studied Cabernet Sauvignon wines made from two different clones, observing differences in their chromatic characteristics. In lemon, improvements in bioactive compounds in the juice, such as vitamin C and flavonoids, may be achieved by selecting specific clones [32]. In a screening of 15 olive tree clones, some were found to have high total polyphenol, oleic and linoleic acid contents [33]. The vitamin C, total carotenoid, total anthocyanin, yellow flavonoids and polyphenol contents and total antioxidant capacity were analyzed in clones of cashew apples, and differences were found between clones [34,35]. Dietary fiber and phenolic compounds were also found to be high in selected clones of acerola and cashew apple [36]. Also in acerola, six commercial clones were investigated by Sampaio *et al.* [37], who found that the clone II 47/1 had the highest anthocyanin content. Oliveira *et al.* [38], studying five acerola clones, established that clones II 47/1, BRS 237, and BRS 236 presented outstanding results for vitamin C, phenols and antioxidant enzyme activity.

Genetic engineering has been used to modify flavonoid biosynthesis in plant tissues [39]. Using structural flavonoid genes from different plant sources, Schijlen *et al.* [40] were able to produce transgenic tomatoes that accumulated new phytochemicals such as high levels of stilbenes, deoxychalcones, flavones and flavonols. The resveratrol content of tomatoes has been increased by metabolic engineering in order to improve their nutritional value. Tomato plants synthesizing resveratrol were obtained via the heterologous expression of a grape (*Vitis vinifera* L.) cDNA encoding for the enzyme stilbene synthase. The transgenic plants accumulated trans-resveratrol and trans-piceid in their skin and had a higher antioxidant capacity and ascorbate content than the wild tomato [41]. In addition, metabolic engineering of the flavonoid biosynthesis pathways in apple was performed by overexpressing the maize leaf color regulatory gene in the mentioned fruit. Higher levels of the anthocyanin idaein (12-fold), of epicatechin (14-fold) and of catechin (41-fold) were found in the transgenic lines [42]. However, genetic transformation is tedious and is expensive, and involves many regulatory issues, not to mention the problem of public acceptance.

3. Phenolic Compounds and Induced Resistance in Plants

Although elicitors were first used to increase plant resistance to pathogens, it was found that the mechanism involved increased polyphenol levels. Consequently, elicitors can be regarded as an interesting alternative for obtaining plants with higher polyphenol content.

Disease resistance in plants is dependent on both pre-existing physical or chemical barriers (such as thick cell walls or high quantities of lignin or tannins) and inducible defense mechanisms. Upon recognition of the attacker, inducible defenses are activated at the site of infection as well as in distant uninfected tissues. Depending on the type of attack, the plant activates different signaling pathways to synthesize a specific set of defensive compounds [43].

The resistance process, mediated by the accumulation of endogenous salicylic acid (SA), a metabolite downstream the biosynthetic pathway initiated by phenylalanine ammonialyase (PAL), is called systemic acquired resistance (SAR) and is based on the induction of secondary metabolic pathways and the increased synthesis of products, phenolic compounds among them, by this metabolism as a response to pathogen attack [44]. It is assumed that SA acts by inducing: (1) pathogenesis-related proteins such as glucanases, peroxidases and chitinases that may contribute to the resistance via hydrolysis of the pathogen cell wall; (2) an oxidative burst, which triggers the elicitation of phytoalexins with antifungal properties; and (3) the phenylpropanoid pathway by activation of PAL, which leads to the formation of phytoalexins, lignins, and SA. Lignification of the plant cell walls is a mechanism to resist pathogen invasion [45,46].

Besides defenses that are dependent on SA, defense-signaling pathways that are independent of this molecule have also been described. Oxygenated fatty acids (oxylipins) can be potent regulators of defense signaling, especially those known as jasmonates (JA), which orchestrate a large set of defense responses, including the synthesis of new phenolic compounds [43].

Although there are many examples of interaction between the pathways involved in the defense response of plants, the complete process is not clearly understood. JA and SA induce the expression of pathogenesis-related genes and increase resistance to chilling injury in tomato fruit [47]. Methyl jasmonate and SA treatments confer resistance to citrus green and blue molds caused by *P. digitatum* and *P. italicum* in sweet oranges [48]. Tomato fruits treated with SA and ethephon (often used as a substitute of ethylene in triggering the ethylene signaling pathway) showed less decay and disease incidence caused by *Botritis cinerea* [49].

4. The Use of Elicitors

In the absence of any attack, these defense mechanisms may be induced by physical or chemical elicitation. Physical elicitors include, for example, high and low temperatures, and ultraviolet and gamma radiation. The stilbene content of Monastrell grapes irradiated with UV-C light was found to be higher than in control grapes and the final wine made from UV-C-irradiated grapes was about 2- and 1.5-fold enriched in resveratrol and piceatannol, respectively, compared with the control wine [2]. Postharvest treatments involving UV irradiation increased the level of trans-resveratrol in apples [50] and of volatile and non-volatile phenols in blueberries [51]. Cold stress in blood oranges induced transcriptomic modifications directed towards increased flavonoid biosynthesis [52]. Similarly, postharvest carbon dioxide treatments induced proanthocyanidin synthesis in grapes [53].

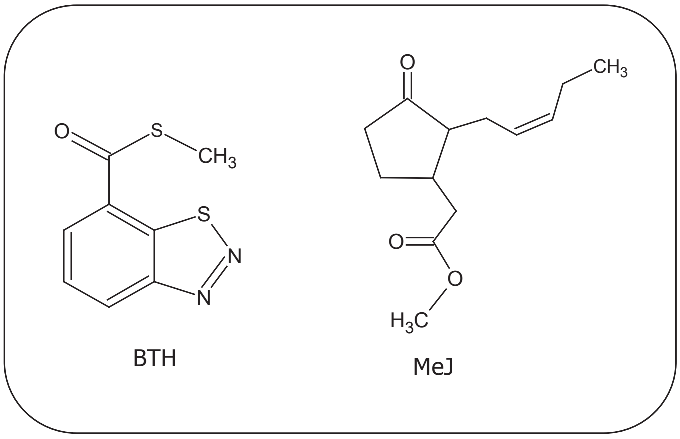
Chemical elicitors, such as chitosan, benzothiadiazole (BTH), harpin, and 1-methylciclopropane, among others, are agrochemicals that can mimic the action of the signaling molecules SA and JA and their derivates, or simulate the attack of a pathogen. These molecules may interact with receptors in the plant, activating defense responses and triggering, in some cases, a hypersensitive reaction. For example, the main resistance substances, such as total phenolics, flavonoids, lignin and hydroxyproline-rich glycoproteins, increased after post-harvest BTH treatment in mangos [54]. The incidence of disease caused by *Penicillium expansum* in BTH-treated peaches was lower than in non-treated ones. Besides the higher resistance, the treated fruits presented higher levels of phenolic compounds, lignin, and chlorogenic acid [55]. The oxidative burst in tomatoes can be elicited by hyphal wall components isolated from *Phytophthora* spp. as an internal emergency signal to induce the metabolic cascade involved in active defense [56]. Foliar application of harpin protein was found to reduce bacterial spots in tomatoes [57]. Chitosan oligosaccharide and Burdock fructooligosaccharide (BFO) were used as elicitors to inhibit natural postharvest diseases and reduce the incidence of disease resulting from inoculation with *Botrytis cinerea* in tomato fruits [58].

For this reason, elicitors were primary designed to improve plant resistance against pathogens. These compounds do not kill pathogens but trigger plant defense mechanisms, among them, the production of increased levels of phenolic compounds. The effect of the application of different elicitors to plants also proved a useful technique for improving their phenolic content. A summary of the effects of different elicitors on plant phenolic composition and phenol-related enzymes is shown in Table 1.

4.1. Benzo(1,2,3)thiadiazole-7-Carbothioic Acid S-*methyl Ester (BTH)*

This compound is an analog of salicylic acid with a molecular weight of 136.17 and with the chemical formula shown in Figure 2. It was synthesized during a project directed at synthesizing sulfonylurea herbicides, where the formation of 2-benzylthio-3-furanylbenzoic acid methyl ester was expected rather than BTH. The ability of BTH in triggering SAR was soon discovered [59].

Figure 2. Chemical structures of the elicitors, benzothiadiazole and methyl jasmonate.



BTH induces the activation of the enzyme PAL, as observed after postharvest treatment in mangoes [60] and peaches [55] (see Figure 1). In both studies, an increase in total phenolic compounds was also observed. Other enzymes from the plant metabolism were activated by this elicitor, including glucose-6-phosphate dehydrogenase, shikimate dehydrogenase, tyrosine ammonia lyase, PAL, cinnamate-4-hydroxylase (C4H), 4-coumarate/coenzyme A ligase (4-CL), and dihydroflavonol 4-reductase (DFR) [61]. Postharvest treatments in bananas and mangoes also resulted in the activation of polyphenol oxidase (PPO) and peroxidases (POD) and an increased total phenolic content [62,63]. However, the effect on flavonoid metabolism might be species-dependent since PAL was inhibited, whereas POD and PPO were activated by postharvest BTH treatment in loquat [64].

Besides the above mentioned studies on enzyme activities, the overall effect of BTH on polyphenolic compounds has been investigated in a variety of fruits. For instance, pre-harvest treatment with BTH of strawberries in greenhouses has proved to be useful for preventing powdery mildew and increasing the content of quercetin and kaempferol [65]; it also enhanced the accumulation of ellagic acid, ellagitannins, p-coumaric acid, gallic acid, and kaempferol hexose in leaves, and kaempferol malonylglucoside in fruits [66], while increasing the amount of quercetin and kaempferol in berries [67]. Field treatments of grapevine with BTH improve resistance to *B. cinerea* and enhance resveratrol and anthocyanin biosynthesis [68]. Similar studies also found an increase in total polyphenols in berry skin, particularly, the proanthocyanidin fraction [44,69], and in the anthocyanin, flavonol, and proanthocyanidin content of grapes and the color of the corresponding wines [70]. Postharvest treatment with BTH resulted in an enhancement of the phenolic and anthocyanin contents of strawberries [71].

Table 1. Summary of the effects of the application of different elicitors on polyphenol content and activity of polyphenol-related enzymes.

Elicitor	Fruit	Preharvest	Postharvest	Activated enzyme and/or increased compound	References
BTH	Mango; peach		Yes	PAL; total phenol content	[55,60]
	Strawberry		Yes	G6PDH, SKDH, TAL, PAL, C4H, DFR, anthocyanins;	[61,71]
	Strawberry	Yes		quercetin and kaempferol; ellagic, *p*-coumaric, and gallic acids	[65–67]
	Banana; mango		Yes	total phenolic content	[62,63]
	Loquat		Yes	POD and PPO	[64]
	Grapevine	Yes		resveratrol, anthocyanins; proanthocyanidins; flavonols	[44,68–70]
MeJ	Lychee		Yes	PAL	[72]
	Peach		Yes	PAL; total phenols	[73]
	Apple, plum, table grape, strawberry		Yes	PAL; total phenols	[74]
	Grapevine	Yes		CHS, STS, UPGT, stilbenes and anthocyanins	[75]
	Red raspberry		Yes	myricetin, quercetin and kaempferol	[76]
	Tomato		Yes	total phenols	[77]
	Pomegranate, strawberry		Yes	total phenols and anthocyanins	[78,79]
	Bayberry		Yes	total phenols	[80]
	Berries; apple; grape	Yes		flavonoids	[70,81–83]
	Strawberry	Yes		resveratrol	[84]
	Grapevine	Yes		resveratrol and viniferins	[85,86]
Harpin	Melon	Yes		PAL, total phenol content, flavonoids, and lignins	[87]
	Jujube		Yes	PAL	[88]
	Peach		Yes	PAL, total phenols	[89]
Chitosan	Table grape	Yes	Yes	PAL	[90,91]
	Banana		Yes	PAL	[92]
	Strawberry		Yes	total phenols	[93]
	Grapevine	Yes		total phenols in grapes and wine	[94]

Table 1. *Cont.*

Elicitor	Fruit	Preharvest	Postharvest	Enzyme activated and/or increased compound	References
Oxalic acid and calcium chloride	Pear	Yes		PAL	[95]
BFO	Tomato	Yes		PAL	[58]
Oligandrin	Tomato	Yes		PAL	[96]
Phosphite and acibenzolar-*S*-methyl	Apple		Yes	*trans*-resveratrol	[50]
Potassium silicate	Avocado		Yes	catechin and epicatechin	[97]

Abbreviations: G6PDH: glucose-6-phosphate dehydrogenase; SKDH: shikimate dehydrogenase; TAL: tyrosine ammonia lyase; C4H: cinnamate 4-hydroxylase; CHS: chalcone synthase; DFR: dihydroflavonol 4-reductase; PAL: phenylalanine ammonia-lyase; STS: stilbene synthase; UPGT: UDPglucose: flavonoid-*O*-transferase (UPGT); BTH: benzothiadiazole; MeJ: methyl jasmonate; BFO: Burdock fructooligosaccharide.

4.2. Methyl Jasmonate (MeJ)

MeJ is a plant volatile derived from JA with a molecular weight of 224.3, whose chemical structure is shown in Figure 2. It has similar activity to JA in plants and so is able to activate the enzymes responsible for the biosynthesis of polyphenols, such as the PAL enzyme (see Figure 1). The activation of PAL following postharvest application of the elicitor has been confirmed in many studies in fruits such as lychees [72], peaches [73], apples, plums, table grapes, strawberries [74] with a subsequent increase of total phenols. The activation of CHS, STS, UDP glucose: flavonoid-*O*-transferase (UPGT), proteinase inhibitors and chitinase gene expression has also been reported in pre-harvest treatments of grapevine with MeJ. Such activations triggered the accumulation of both stilbenes and anthocyanins in cells [75]. In a different fruit, red raspberry, the enhancement in the levels of myricetin, quercetin and kaempferol has also been reported after postharvest treatment with MeJ [76].

Several other studies on different fruits describe how MeJ affects polyphenol compounds. For example, postharvest treatment with MeJ resulted in higher amounts of total phenols and anthocyanins in tomatoes [77], pomegranates [78], strawberries [79], and bayberries, in which an increase of other flavonoids was also found [80]. Finally, pre-harvest treatment with MeJ has been shown to enhance the levels of flavonoids in blueberries [81], blackberries [82], apples [83], and grapes [70]; and resveratrol levels in strawberries [84] and grapevine cultivars [85,86].

4.3. Harpin

Harpin is a heat-stable, glycine-rich protein of bacterial origin. This protein was first described as being produced by the plant pathogen *Erwinia amylovora* that causes fire blight in pear, apple and other rosaceous plants [98]. Harpin is able to provoke a hypersensitive response in non-host plants. This response is characterized by a rapid localized cell death at the site of the invasion [99], for which reason, it is able to act as a chemical elicitor. Moreover, this protein activates ROS burst, SA and the JA/ethylene signal transduction pathways that confer SAR to different plants [100–102]. Harpin has been applied as an effective postharvest treatment to prevent decay in oranges [103], melons [104], apples [105] and pears [106]. In addition, field applications demonstrated its usefulness for controlling pathogen-borne diseases in passion fruits [107], pears [108], quince and loquat [109].

Harpin has also been described as an elicitor able to activate enzymes such as PAL from the polyphenol biosynthesis pathway. Examples of this have been found in several fruits; for instance, in postharvest-treated peaches and jujube, with a subsequent increase in total phenols [88,89]. In addition, in melon, field application produced enhanced levels of phenolic compounds, flavonoids and lignin [87].

4.4. Chitosan

Chitosan is a polysaccharide resulting from the deacetylation of chitin, the linear polymer of (1-4)-β-linked *N*-acetyl-D-glucosamine. It is obtained from the outer shell of crustaceans such as crabs and shrimps. This polysaccharide has a positive charge that confers specific physiological and biological properties that are found useful in different industries such as the cosmetics, food, biotechnology, pharmacology, medicine and agriculture industries [110]. Even though it has antimicrobial properties, there is strong evidence that it can act as an elicitor by inducing the production of callose and phenolics in susceptible plants [46].

The extent of the antimicrobial action of chitosan is influenced by factors such as its molecular weight (MW) and degree of acetylation (DA). However, it is difficult to find a clear correlation between these two characteristics and the antimicrobial activity. In general, as the DA increases, the antimicrobial activity is enhanced, since chitosan with a high DA dissolves in water completely, leading to an increased chance of interaction between chitosan and the negatively charged cell walls of micro-organisms. Similarly, as the MW increases, chitosan activity against pathogens increases, but, above a certain value, the effect is reversed [111,112].

Applications of chitosan in the field proved to be effective in controlling postharvest diseases in strawberries [113,114] and in jujubes, where it activated defense-related enzymes to reduce postharvest decay [90]. Postharvest applications of a coating composed of chitosan and *Origanum vulgare* L. essential oil at sub-inhibitory concentrations were able to control *Rhizopus stolonifer* and *Aspergillus niger* in grapes [91].

Many pre- and post-harvest treatments with chitosan have demonstrated that this compound can activate the enzyme PAL (see Figure 1) and increase total polyphenols in table grapes, controlling storage gray mold [92], and activating PPO [93]. It may also enhance the activity of defense-related enzymes in bananas [94] and increase the amount of total polyphenols in strawberries [95]. In addition, chitosan has proved to be effective at controlling powdery mildew and at increasing the total polyphenol content of grapes. Moreover, wines made from chitosan-treated grapes showed a higher total polyphenol content and antiradical power than those made from fungicide-treated and untreated grapes [96].

4.5. Other Elicitors

Many other chemical substances have been studied as possible elicitors in different fruits. For example, oxalic acid and calcium chloride enhanced defense-related enzyme activities, such as β-1, 3-glucanase, PAL, POD and PPO, and reduced disease incidence caused by *Alternaria alternata* in pears [97]; Burdock fluctooligosaccharide and oligandrin inhibited postharvest disease caused by B. *cinerea* in tomatoes and activated PAL, enhancing the biosynthesis of phenolic compounds [58,115]; phosphite and acibenzolar-*S*-methyl induced the synthesis of trans-resveratrol in apples [50], and finally, potassium silicate increased the amounts of catechin and epicatechin in avocados [116].

5. Conclusions

Polyphenolic compounds are important for plants and humans for many reasons: they protect the plant from biotic and abiotic stressors, they contribute to some organoleptic and quality properties in food, they are a unique source of industrial material for uses as food additives, pharmaceuticals, and flavors; and they are considered beneficial for health because of their antioxidant capacity. Fruits are one of the most important sources of polyphenols for humans. The use of elicitors may be regarded as a simple and useful technique to increase the phenolic content of fruit, protecting, at the same time, both plants and fruits from biotic and abiotic stresses, without the disadvantage of the environmental impact and risk of creating resistant pathogen strains that may result from using conventional herbicides and antifungal or antimicrobial compounds.

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