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*Review*

# Application of Elicitors in Grapevine Defense: Impact on Volatile Compounds

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**Abstract:** Elicitors as alternatives to agrochemicals are widely used as a sustainable farming practice. The use of elicitors in viticulture to control disease and improve phenolic compounds is widely recognized in this field. Concurrently, they also affect other secondary metabolites, such as aroma compounds. Grape and wine aroma compounds are an important quality factor that reflects nutritional information and influences consumer preference. However, the effects of elicitors on aroma compounds are diverse, as different grape varieties respond differently to treatments. Among the numerous commercialized elicitors, some have proven very effective in improving the quality of grapes and the resulting wines. This review summarizes some of the elicitors commonly used in grapevines for protection against biotic and abiotic stresses and their impact on the quality of volatile compounds. The work is intended to serve as a reference for growers for the sustainable development of high-quality grapes.

**Keywords:** benzothiadiazole; chitosan; grapes; grape-derived aromas; methyl jasmonate

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## 1. Introduction

Grapevine (*Vitis vinifera* L.) is one of the essential fruit crops cultivated globally for its economic and health benefits. The primary product, grapes, are consumed as fresh fruits or juice (table grapes) or processed into wines (wine grapes) [1]. The quality of grape products, especially wine, is influenced mainly by the primary and secondary metabolites of the grapes [2,3]. However, these metabolites are affected by several pests and diseases as well as vine management practices and many other factors (e.g., soil, climate, weather).

The main aim of grape producers in the past was to enhance grape productivity and obtain a good yield to meet the high demand for wines. Therefore, different strategies, such as the use of fungicides and pesticides and other management practices, were employed to prevent any biotic or/and abiotic stresses that could decrease yield [4–6]. However, the use of fungicides and pesticides has adverse effects on human health and the environment. Excessive usage causes residual buildup in soils, plants, and groundwaters, affecting beneficial soil organisms, humans, and the environment, while continual use leads to pathogen resistance [7,8].

Although it is necessary to prevent grape diseases and infections, adverse effects on fruit yield and quality must be avoided. In addition, there has been more emphasis recently on achieving sustainable quality yields through "green production." Under this term, the European Commission has recently announced measures aimed at achieving healthy and environmentally friendly food production by 2050 [9,10]. This includes reducing the use of pesticides and fungicides. According to the FAO [11], the world population will grow to 9.7 billion by 2050. To prevent food shortages and ensure the sustainable development of high-quality food, environmentally friendly methods are currently being increasingly used, as opposed to pesticides and fungicides.

Elicitors are stress stimuli capable of inducing similar defense responses in plants as induced by the pathogen infection [5,7]. Elicitors induce plant resistance against pathogens by activating signals that enhance the production of secondary metabolites. Elicitors are of different types; chemical elicitors such as benzothiadiazole or methyl Jasmonate, physical elicitors such as light, salinity, or temperature, and elicitors of biological origin, such as oligosaccharides, yeast derivatives, or protein fragments [12,13]. The use of elicitors as alternatives to agrochemicals in preventing grape diseases and infections also has a great impact on the quality components of grapes [14,15]. Numerous studies intending to improve wine aroma quality have investigated the effects of different elicitors on the volatile compositions of grapes. However, their impact varies depending on several factors such as grape cultivar, type of elicitor, and dose.

Under this framework, the main focus of this review is to provide an overview of some of the commonly used elicitors in grapevines and their impact on the quality of grape-derived aroma compounds. The work is intended to serve as a reference for growers for the sustainable development of high-quality grapes using elicitors.

## 2. Grape Composition

Grape quality is primarily assessed by the compositional chemical measures of the grape, such as the pH, sugars, titratable acidity, color (for red grapes), aroma compounds, phenolic compounds, and other volatiles [16,17]. These chemical parameters are influenced by the different vineyard soil conditions, climate conditions, and vine management practices and changes throughout the development period [2,17,18]. The credibility of these parameters, especially the sugar content of grapes as a qualifier of "quality" at harvest, is not a point of contention [19,20]. Sugar as a primary metabolite also influences several secondary metabolites, especially the concentrations of aroma compounds [21,22]. According to Rolland et al. [23], soluble sugars also function as signaling molecules aside from their impact on the overall sensory quality of fruits. They modulate genes involved in defense and metabolic processes, thus, affecting fruit maturity and the biosynthesis of secondary metabolites.

### *2.1. Grape-Derived Aroma Compounds*

Aroma is an essential characteristic that varies significantly with grape maturity and ultimately determines the grape and wine quality. The aroma components of wine are an important factor that reflects the nutritional information of the wine and influences consumer liking [24]. Depending on the origin of aroma compounds, they are classified either as primary, secondary, or tertiary aromas [25]. The varietal (primary) aromas are derived from grapes and vary depending on the cultivars, climate conditions, and vineyard practices [4]. Aromas produced during maceration and fermentation are known as secondary aromas, while tertiary aromas are formed during the aging of wine [4]. Grape-derived aromas are found both in the skin and the pulp [26], with a low human detection threshold [27]. Grapes consist of hundreds of volatile compounds, some of which are present in free odor-active forms, and the majority are found in glycosylated form, serving as potential aroma reservoirs [28].

### 2.1.1. Terpenoids

Terpenoids, among the various classes of grape-derived aromas, are the most studied volatile compounds. Terpenoids are grouped according to their carbon numbers into hemiterpenes ($C_5$), monoterpenes ($C_{10}$), sesquiterpenes ($C_{15}$), diterpenes ($C_{20}$), and tetraterpenes ($C_{40}$), with monoterpenes ($C_{10}$) as the dominant class [4,29,30]. Grapes are categorized into Muscat, non-Muscat aromatic, and neutral varieties based on their monoterpene concentration levels [24]. Monoterpenes are synthesized through the mevalonic acid (MVA) pathway and the methylerythritol phosphate (MEP) pathway from isopentenyl diphosphate (IPP) and dimethylallyl diphosphate (DMAPP). Thereafter, through the activity of terpene synthases (TPS), monoterpenes are formed from 2-(E)-geranyl diphosphate

(GPP) [31]. However, among the two biosynthetic routes, the MEP pathway is said to be the prime route for the formation of terpenoids in grapes [32]. Terpenoids are stored as free and bound volatiles, mainly in the grape skin, with trace concentrations in the pulp [4,30]. Climate, management practices such as grape shading, elicitation, and many other factors (e.g., pruning, irrigation, fertilization) influence the concentrations of terpenes, as reported in the literature [33–35]. For instance, concentrations of monoterpenes in Sauvignon blanc grapes decreased with high canopy density [36], while the concentration of these molecules increased when Sauvignon blanc grapes were exposed directly to the sun after leaf removal [37].

### 2.1.2. Norisoprenoids

Norisoprenoids are volatile compounds of 9, 10, 11, or 13 carbon cyclic chemical structures derived from carotenoids [4,38,39]. Carotenoids are pigments produced in the chloroplast and decline during grape ripening due to the unavailability of the chloroplast [40–42]. Hence, decreasing the norisoprenoids synthesized. Norisoprenoids are formed through the conversion of biodegraded carotenoids by enzymes to the aroma precursor and subsequently to the aroma-active compound by the acid-catalyzed conversion [4,30,38,40,41]. Norisoprenoids are grouped into megastigmane and non-megastigmane forms, with most norisoprenoids in the megastigmane form differing based on the position of the oxygen functional group [4,38]. $C_{13}$-norisoprenoids are the abundant norisoprenoids in grapes, with β-ionone, β-damascenone, vitispirane, actinidiol, 1,1,6-trimethyl-1,2- dihydro naphthalene (TDN), and 2,2,6-trimethylcyclohexanone (TCH) as the most prevalent compounds conferring fruity and floral notes [4,30]. Grape-derived norisoprenoids are affected by vineyard management practices such as leaf removal, cover cropping, irrigation, and many other factors (e.g., fertilization, grape shading) [39,43,44].

### 2.1.3. Methoxypyrazines (MPs)

Nitrogen-containing grape-derived volatiles, 3-Alkyl-2-methoxypyrazines (MPs), are found abundantly in the stems (79.2%) rather than in the berries (20.8%) [45]. The precise biosynthesis pathway of MPs is still unclear, although they are suggested to be derived from the metabolism of amino acids [4,30]. However, the last step in the synthesis of MPs (O-methyltransferases (OMT) methylation of hydroxypyrazine precursors to methoxypyrazines) is explicit, as several identified genes correlated positively with the precursors [46–49].

The most important MPs, 2-methoxy-3-isobutylpyrazine (IBMP), 2-methoxy-3-sec-butylpyrazine (SBMP), and 2- methoxy-3-isopropylpyrazine (IPMP), out of the seven detected in grapes, impact grassy, herbal, bell pepper, leafy, and asparagus-like odorants in several wines such as Cabernet Sauvignon, Sauvignon Blanc, Chardonnay, Cabernet franc, Carmènere, and Merlot [33,49–52]. The most abundant among the three important MPs is IBMP, mostly found in the grape skin [4,45]. Koch et al. [53] studied the accumulation of IBMP in 29 different grapes and reported high levels of IBMP in some cultivars compared to trace levels or undetected IBMP in other cultivars. Several studies have shown that grape variety and other factors such as maturity, climate, leaf removal, and light exposure [39,50,54–56] influence the accumulation and concentrations of MPs.

### 2.1.4. Fatty Acids Derivatives

Fatty acid-derived volatiles, including alcohols, aldehydes, ketones, lactones, esters, and acids, constitute the majority of volatile compounds in grapes [38,42]. These compounds are synthesized through the α-oxidation, β-oxidation, or lipoxygenase pathways [42]. $C_6$ aldehydes and alcohols are the most abundant compounds among these derivatives. The $C_6$ compounds are produced from linoleic and linolenic acids enzymatically by lipoxygenase (LOX), hydroperoxide lyase (HPL), (3Z), (2E)-enal isomerase, and alcohol dehydrogenase (ADH) thru the LOX pathway in damaged and crushed grape tissues [42,57]. $C_6$ compounds are partly responsible for the green, herbaceous odorant in grapes and grape products. The concentrations of $C_6$ compounds are varietal dependent [58,59] and also influenced by maturity [39,59,60] and season [59,61]. The concentrations of the $C_6$ compounds in most of these studies were high during the pre-veraison and veraison stages but started to decline after veraison. However, this was not the case for all the studies. For example, in the study reported by Salifu et al. [60], they observed decreasing concentrations of all $C_6$ aldehydes and alcohols from the pre-veraison to maturity stages, except for 1-hexanol, which observed higher concentrations during the pre-veraison and maturity stages. Likewise, the study on Pinot noir grapes by Yuan and Qian [39] reported continuous decreasing concentrations of $C_6$ alcohols after the veraison stage. These observations affirm that grape variety influences the concentrations of $C_6$ compounds.

### *2.2. Grape Amino Acids*

Amino acids are vital not only for the synthesis of proteins but also as precursors for the production of aroma compounds [62,63], signaling molecules [64], and triggering defenses against biotic and abiotic stresses [65,66]. Amino acids are the main nitrogenous compounds in grapes (approximately 25–30%) amassed in the skin, seeds, and pulp [67–69]. The composition and concentration of amino acids vary with vintage, grape variety, level of maturity, and soil fertility [70–74]. In relation to the cultivar, previous works [74–76] observed that total amino acids concentration in white grapes was higher than total amino acids concentration in red grapes, and within the red grape varieties, those with relatively high chroma (measure of anthocyanins) had low total amino acids concentration compared to varieties with low chroma. According to Guan et al. [77], the inverse relation of the color index and concentrations of amino acids from a metabolic viewpoint hypothesized that the high color index could be at the expense of amino acid precursors (C-skeleton). Furthermore, the nutrient status of the vine, especially the nitrogen level, greatly impacts the composition of grape amino acids, as observed by these authors [70–73,78].

## **3. Elicitors and Their Classifications**

Elicitors protect plants against biotic and abiotic stresses by mimicking the plant's metabolic responses triggered by pathogen infection [79–81]. Elicitors do not kill pathogens but cause plants to stimulate their innate resistance to subsequent attacks. This response of plants against subsequent attacks has been termed differently by several researchers [80,82,83]. These include induced systemic resistance (ISR) or systemic acquired resistance (SAR), which involves the accumulation of phytoalexins and pathogen-related proteins and the thickening of plant cell walls [5,83]. According to Azmina et al. [82] and Romera et al. [84], SAR is associated with pathogens, while ISR is related to beneficial microorganisms. Compared to conventional agrochemicals, elicitors are eco-friendly and non-toxic. Moreover, a low concentration is sufficient to enhance the synthesis of secondary metabolites and protection against a wide array of pathogens [85].

Elicitors are classified differently based on their origin (plants or microorganisms), molecular structure (general or specific), and nature but are generally grouped under biotic and abiotic [5,7,81,83]. All elicitors originating from microorganisms are biotic, and depending on the stress type, they can be classified either as endogenous or exogenous. Physical and chemical elicitors are abiotic in nature and have no biological origin. Thakur and Sohal [5] further categorized elicitors based on their structures as general and specific elicitors. While general elicitors can induce defense in host and non-host plants, specific elicitors can only trigger defense in host plants. Precisely for specific elicitors, the pathogen and host plant have complementary pairs of genes. Thus, the infectious gene present in the pathogen triggers resistance only in a host plant with the corresponding complementary gene [5]. That means the absence of the complementary gene in the plant will result in disease. However, the relative nature of general elicitors is restricted and not recognized by all plants. Plant hormones such as jasmonic acid and salicylic acid are also considered elicitors [80]. The various classifications of elicitors are shown in Figure 1.

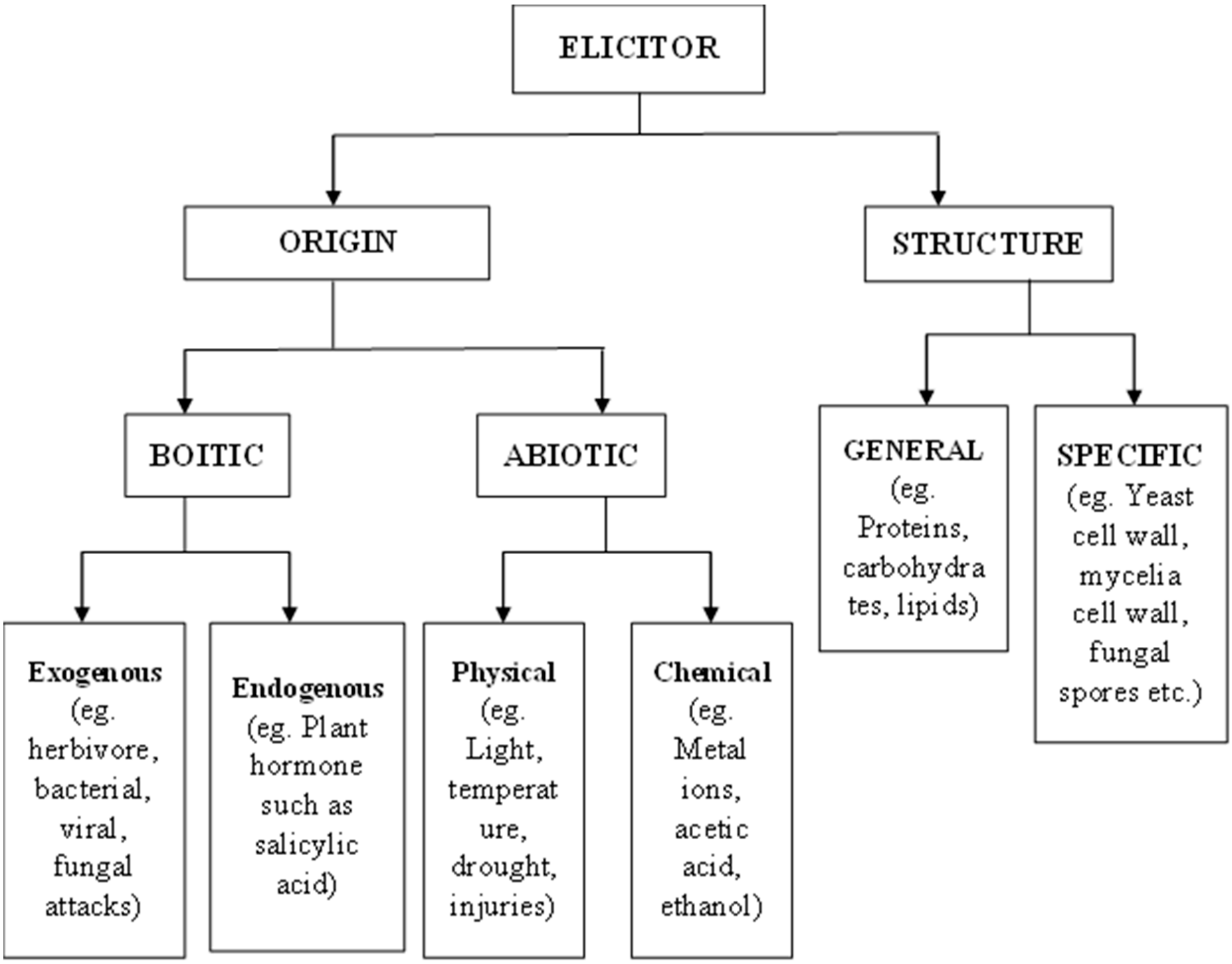

**Figure 1.** Classifications of elicitors.

### 3.1. Mode of Action

Initially, elicitor was a term used only for molecules that were capable of producing phytoalexins. However, substances capable of triggering any form of defense in plants are now also referred to as elicitors [5]. Recent understanding of the plant immune system shows that the first step of the innate response of plants to elicitors is the perception of the stimulus by pattern recognition receptors (PRRs) located in plants (plasma membranes or within cells) [82,86]. These pattern recognition receptors (PRRs) detect pathogen-associated molecular patterns (PAMPs) and activate PAMP-triggered immunity (PTI), a local defense mechanism that halts the colonization of pathogens by the induction of mitogen-activated protein kinases (MAPK) [80], the production of reactive oxygen species (ROS), reactive nitrogen species (RNS), ion fluxes, among other defense responses [87,88].

In the next phase, signaling molecules such as salicylic acid, jasmonic acid, and ethylene (SA, JA, and ET) trigger reactions to protect the plant from subsequent attacks [5,14,80,82,83,89]. Effector-triggered immunity (ETI), unlike PTI, deals with modified pathogens (effector molecules) that act as potential pathogen indicators [82,83,89]. Once resistance proteins identify these indicators (effectors), ETI will activate and induce immune responses. The induction of ETI results in the death of tissues in the infected region, preventing the spread of infection to other parts of the plant, a phenomenon known as the hypersensitive response (HR) [90]. As a result, the plant acquires increased resistance to subsequent infections through the signal transduction pathways [82,90].

SAR is one of the defense pathways of plants against infectious attacks, and this response is activated and expressed throughout the plant tissues on account of a previous pathogen attack [82,83,90]. The induction of SAR occurs through the buildup of salicylic acid (SA), a phytohormone that uses the protein Non-Expressor of Pathogenesis-Related Genes 1 (NPR1) to stimulate the expression of pathogenesis-related (PR) genes [83,84]. Pathogenesis-related (PR) genes are a group of plant defense genes responsible for the accumulation of phytoalexins, the production of pathogenesis-related proteins, cell wall reinforcement, and others [5]. Figure 2 shows the general response mechanisms of plants to elicitors.

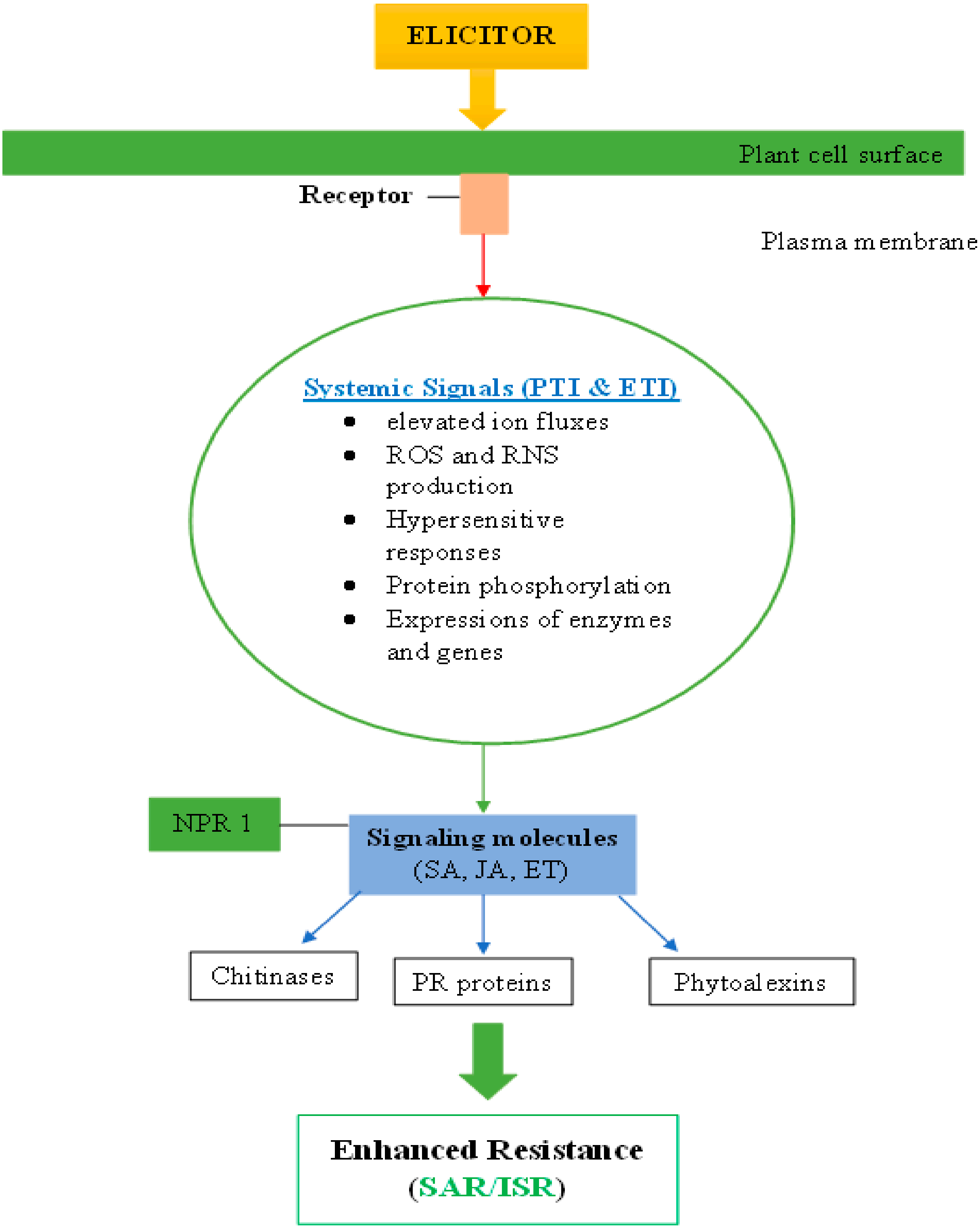

**Figure 2.** General mechanisms of plant responses to elicitors.

### *3.2. Uses of Elicitors*

To control pests and diseases in grapevines while maximizing fruit yield and enhancing quality, the use of elicitors as a tool to enhance the immune system and metabolite content in grapes is on the upsurge [14,91]. Several studies have reported various types of elicitors and their influence on grapes [5,14,92]. Elicitors can be applied separately or in combination at specific period(s) of the vine's physiological state. Due to the antagonistic activities of elicitors, the suppression or activation of metabolic pathways regulates the grapevine responses [80]. The combined use of two or more elicitors depends on their efficiency, which negatively or positively affects the plant response as the signaling pathways could provoke or complement each other [80,93,94]. The type of elicitor, concentration, and treatment time may affect grapevine responses in different ways. However, grape genetics and other factors (Figure 3) play an equally significant role [8,80]. For instance, the concentration of secondary metabolites induced by the stimulation of elicitors depends on grape genetics. Thus, the impact of different or same elicitors on grapes of the same or different species varies.

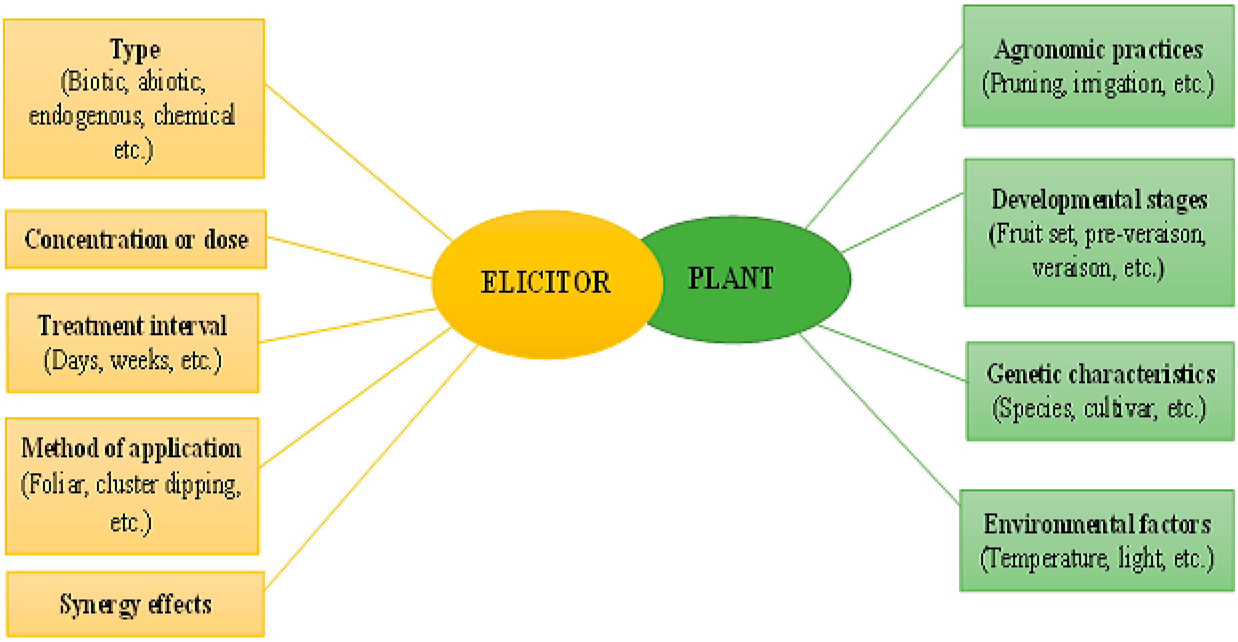

**Figure 3.** Factors influencing the production of secondary metabolites in plant-elicitor interactions.

### *3.3. Elicitors Commonly Used on Grapevines*

Different classes of pathogens infect grapevines, reducing grape yield and quality. Fungi (*Botrytis cinerea*) and oomycetes (*Erysiphe necator* and *Plasmopara viticola*) are the most persistent classes causing gray mold, powdery mildew, and downy mildew in grapes, respectively. These and several other diseases were initially treated and prevented with fungicides. Nevertheless, due to the negative impact of fungicides on the environment and the resistance of causative agents to fungicides [8,92], elicitors are currently used as alternative preventive measures. However, the impact of elicitors on grapes is beyond the protection function. They also influence the volatile composition and sensory characteristics of grapes and wines. Several studies have reported the effective resistance induced by grapevine elicitors against diseases (Table 1) and their impact on the metabolites of elicited grapes (Table 2). Subsequent subsections of this review focus on some of the commonly used grapevine elicitors.

**Table 1.** List of Some Elicitors and their Defense Impact on Different Grape Cultivars.

| Elicitor | Grape | Defense Response | Reference |
|---|---|---|---|
| BTH, Laminarin (Lam), Potassium phosphonate (K-Pho) | Moscato, Nebbiolo | All products reduced disease incidence; significantly reduced disease severity; Moscato was less susceptible to the disease than Nebbiolo | [95] |
| Nano-Methyl Jasmonate | Monastrell | Increased phytoalexins synthesis and lower cytotoxicity than MeJ | [96] |
| Ozonated water | Bobal | limited grapevine infection by *Phaeoacremonium aleophilum* | [97] |
| COS-OGA | Carignan | Induced 78% protection of grapes against powdery mildew in France and 76% in Spain | [98] |
| Flagellin and harpin | Pinot noir | ROS production; accumulation of phytoalexins; induction of defense genes; blocked extracellular alkalinization | [99,100] |
| Rhamnolipids | Gamay and Chardonnay | Inhibited spore germination and mycelium growth of *Botrytis cinerea*; SA synthesis; phytoalexin accumulation | [101] |
| Sulfated laminarin (PS3) | Marselan | PS3 induced resistance against downy mildew under greenhouse conditions; elicited the emission of Volatile organic compounds; increased antimicrobial activity | [102,103] |
| Cellodextrins (CD) | Chardonnay | $H_2O_2$ generation; increased calcium flux; ROS production; stimulation of chitinase and β-1,3 glucanase activities | [104] |
| Chitosan | Chardonnay | Increased PAL and chitinase activities; reduced gray mold and downy mildew infections; increased stilbenes and phytoalexins accumulations | [105–107] |
| Cyclodextrins | Gamay | Accumulation of phytoalexin; peroxidase activity induction | [108] |
| Ergosterol | Ugni Blanc | Enhanced protection against *Botrytis cinerea* | [109] |
| Benzothiadiazole (BTH) | Merlot | Enhanced trans-resveratrol content, anthocyanin synthesis; induced SAR; decreased *Botrytis cinerea* infection; increased total polyphenols | [110,111] |
| *β*-aminobutyric acid (BABA), Jasmonic acid (JA) | Chasselas and Solaris | Callose and lignin deposition; increased resistance against downy mildew; expression of LOX-9 and PR-4 genes | [112] |
| Methyl Jasmonate (MeJ) | Cabernet Sauvignon | Induction of peroxidase, chitinase, and, glucanase activities; phytoalexin accumulation | [113] |
| Ethephon | Cabernet Sauvignon | Increased number of PR-proteins; enhanced phytoalexin biosynthesis; induced protection against *Erysiphe necator* | [114] |
| Soybean and casein hydrolysates | Marselan | Enhanced grapevine immunity against *Plasmopara viticola* attack | [115] |
| Methyl Jasmonate (MeJ) | Barbera | Increased berry resveratrol and ε-viniferin production | [116] |

**Table 2.** Influence of Some Elicitors on Grape and Wine Quality.

| Elicitor | Grape | Impact on Quality | Reference |
|---|---|---|---|
| Methyl Jasmonate (MeJ) | Hamburg Muscat (Black Muscat) | MeJ activated terpenoid biosynthesis pathway; increased concentrations of free and glycosylated monoterpenes in grapes and wine; improved aroma quality | [117] |
| Nano-Methyl Jasmonate (nano-MeJ) | Monastrell | Significant increase of beneficial stilbenes (*trans*-resveratrol, *cis*- and *trans*-piceid) | [96] |
| Ozonated water | Bobal | Improved chromatic characteristics; favored the accumulation of phenolic compounds; increased some free volatile aromas; generally improved grape quality | [97] |
| Methyl Jasmonate (MeJ) | Tempranillo | MeJ improved the synthesis of p-cymene, methyl jasmonate, and hexanal (1st vintage) while diminishing the content of some $C_6$ alcohols, esters, several terpenes, and β-damascenone in the 2nd vintage; several positive aroma contributors were improved in the 3rd vintage | [118] |
| Methyl Jasmonate (MeJ), chitosan (CHT), and yeast extract (YE) | Tempranillo | CHT and YE decreased the concentrations of several amino acids while MeJ increased the concentrations of most amino acids especially Met and Phe; All treatments decreased the synthesis of grape volatile compounds | [35,67,119] |
| Methyl Jasmonate (MeJ) | Sangiovese | Delayed maturity, increased concentrations of several grape aroma classes, a rise in wine aroma concentrations with improved sensorial characteristics | [61] |
| Methyl Jasmonate (MeJ) and Phenylalanine (Phe) | Grenache | Both elicitors enhanced the volatile content of grenache grapes; MeJ improved terpenoids and $C_{13}$ norisoprenoids; most of the positive compounds were enhanced by Phe treated; Phe + MeJ increased concentrations of most volatiles | [120] |
| Methyl Jasmonate (MeJ) | Graciano and Tempranillo | MeJ increased the concentrations of several amino acids in Graciano; decreased the content of some amino acids in Tempranillo but did not affect the total amino acids content | [121] |
| Benzothiadiazole (BTH) and MeJ | Monastrell | No effect on alcohols and esters; increased concentrations of terpenes; synthesis of some terpenes only in treated wines; improved sensory qualities; increased levels of phenolic compounds | [122–125] |
| BTH and chitosan (CHT) | Groppello | CHT improved the volatile profile, flavor, and taste of Groppello wine, increased total acetals, and alcohols; BTH increased total acetals and esters | [126] |

### 3.4. Chitosan (CHT)

Chitosan is a cationic polymer derived from the polymeric polysaccharide chitin. Chitosan can be applied directly to plants in a liquid state or the soil in powdery or liquid form [127]. Chitosan induces several beneficial responses in plants due to its cationic nature. The antimicrobial, antifungal, among other properties of chitosan, prevent pathogens from accessing mineral nutrients by disrupting potassium signaling in pathogens and preventing the pathogens from releasing mycotoxins [128–130]. Chitosan, through several investigations, has proven efficient in controlling grape pathogens, especially gray mold and powdery mildew, distressing grapevine diseases caused by *Botrytis cinerea* and *Erysiphe necator*, respectively [105–107,131]. Moreover, chitosan's influence on phenolic compounds [132,133], amino acids [119], volatile compounds [35,126], and other metabolites [12,134] has also been studied. According to some of these studies, chitosan treatment positively and negatively affected some quality parameters. For example, in the study reported by Gutiérrez-Gamboa et al. [119], they observed a significant decrease in the concentration of amino acids in chitosan-treated grapes compared to the control grapes. Irrespective of the grape cultivar and other factors, the effectiveness of chitosan treatment depends on the variations in the chitosan extraction and modification processes, such as the length of the polymer, the degree of acetylation, etc. [127,135]. Differences in these factors have resulted in different chitosan treatment responses in grapes, as cited in the literature [12,126,134].

### *3.5. Methyl Jasmonate (MeJ)*

Methyl Jasmonate (MeJ) is an elicitor capable of triggering the synthesis of secondary metabolites by inducing plant defense mechanisms [136]. Methyl Jasmonate (MeJ), as a derivative of jasmonic acid (JA), is widely used in viticulture due to its significant impact on grape metabolites such as volatile compounds [35,61,120,137]. Most recent MeJ studies are focused on the phenolic and volatile contents of grapes and wines since these compounds influence their sensorial quality to a greater extent. D'Onofrio et al. [61] and Román et al. [120], in their studies of MeJ application to Sangiovese and Grenache grapes, reported an increase in the concentration of volatile compounds in the treated samples compared to the respective control samples. However, after treating Tempranillo grapevines with MeJ, grape volatiles concentrations in the treated samples decreased relative to the control samples [35]. An indication that grape variety is a factor influencing the effectiveness of MeJ. Similarly, a study on the impact of MeJ on the concentrations of grape amino acids was influenced by variety and vintage [121].

In the context of phenolic compounds, the grape variety is not a limiting factor, as most studies have reported increased levels of phenolic compounds after MeJ application, irrespective of the variety [124,125,138,139]. However, seasonal variations impact the effectiveness of MeJ on grape quality components, especially in consecutively studied seasons. Methyl Jasmonate (MeJ) often improves the content of metabolites in one season and decreases the levels in the subsequent season, as reported in the following studies [121,125,136,137,139]. Regarding the time of treatment, MeJ, like other elicitors, is usually applied on grapes during the veraison stage. However, few studies sprayed MeJ on grapevines during veraison and mid-ripening and reported that phenolic compounds were enhanced better in samples treated during mid-ripening than samples treated during veraison [140,141]. Hence, they postulated that the optimum time for MeJ application could be a few weeks after veraison.

### *3.6. Benzothiadiazole (BTH)*

Benzo (1,2,3)-thiadiazole-7-carbothioic acid S-methyl ester (BTH), as reported in the literature, was isolated from a synthesis project aimed at isolating 2-benzylthio-3-furanylbenzoic acid methyl ester instead of BTH [142–144]. However, the authors discovered that BTH could trigger defense mechanisms in plants against several infections [142]. Benzothiadiazole, as a chemical elicitor, induces responses similar to the endogenous plant hormone salicylic acid (SA) at the molecular level. Thus, BTH is said to be a functional analog of salicylic acid (SA) that induces the activation of several enzymes, especially PAL, triggering the syntheses of bioactive secondary metabolites [21,111,134,144,145].

The application of BTH in viticulture has proven efficient in enhancing the polyphenol contents of grapes and their resulting wines in different grape varieties. BTH application to Monastrell grapevines at different ripening stages increased the accumulation of anthocyanins (in treated grapes) in both studied seasons [140]. Similarly, in the previous work by Paladines-Quezada et al. [137], an increase in the concentrations of anthocyanins and flavonols was reported in Monastrell BTH-treated grapes and wines compared to their respective control samples. Moreover, the application of BTH to different grape varieties improved the phenolic compounds and chromatic characteristics in the grapes and wines of Syrah and Merlot treated samples relative to their respective control samples [138].

These positive influences of BTH on polyphenols contents coupled with induced defense mechanisms in grapes are associated with a metabolic cost [21]. According to Wang et al. [21], the application of BTH reduces the concentrations of primary metabolites in treated grapes, especially the total soluble sugars, which serve as signaling molecules that modulate the set of genes involved in defense and metabolic responses. The authors postulated that the common precursor (UDP-glucose) of the sucrose metabolism pathway and phenylpropanoid pathway might have been directed towards the biosynthesis of polyphenol compounds while reducing the accumulation of soluble sugars. Consequently, the reduced levels of soluble sugars and other primary metabolites such as amino acids influence the volatile compositions and sensory quality of treated grapes and their resulting wines. The extent of the impact on these quality parameters differs with different varieties. Gómez-Plaza et al. [123], in their study of BTH application to Monastrell grapevines, reported a significant increase in the concentrations of various volatile classes, especially terpenoids and norisoprenoids, in BTH-treated grapes compared to the control grapes. Concerning the impact of BTH on wine volatiles, Vitalini et al. [126] treated Groppello Gentile grapevines with BTH for two consecutive seasons. Wines volatile profiles from the treated and untreated grapes were analyzed. The authors reported increased acetals and esters concentrations in BTH-treated wine during the first season and increased total esters concentration only in BTH-treated wine during the second vintage. All other volatile classes recorded low concentrations in BTH-treated wine compared to the wine from conventionally treated grapes in both seasons. However, Gómez-Plaza et al. [123], in their study of Monastrell wines from BTH-treated grapes, reported significant increases in the concentrations of alcohols, esters, terpenes, and norisoprenoids in BTH-treated wine compared to the control wine. Differences in the accumulation and concentrations of volatile compounds (Table 2) in these studies could be attributed to the differences in their primary metabolites as affected by BTH application and several other factors shown in Figure 3.

### 3.7. Influence of Elicitors on Grape Aroma Biosynthesis

Aroma biosynthesis is a complex process that involves different metabolic pathways synchronized during development by several enzymes (Figure 4) [146–149]. External conditions such as elicitation influence the synthesis of volatile compounds [147]. The application of elicitors mainly impacts the composition of grape aroma in two ways. Elicitors modify the biosynthetic pathways, thus, influencing the accumulation and distribution of metabolites. On the other hand, elicitors enhance the absorption of water molecules into the berry cells, causing the size to expand and diluting soluble sugars and other primary metabolites, altering the volatile concentrations [4,150]. Accordingly, the aroma concentrations either increase or decrease depending on the skin-to-pulp ratio of the berry as influenced by the berry size because the grape skin is the essential site for the synthesis and storage of volatile aromas in large quantities [3,151].

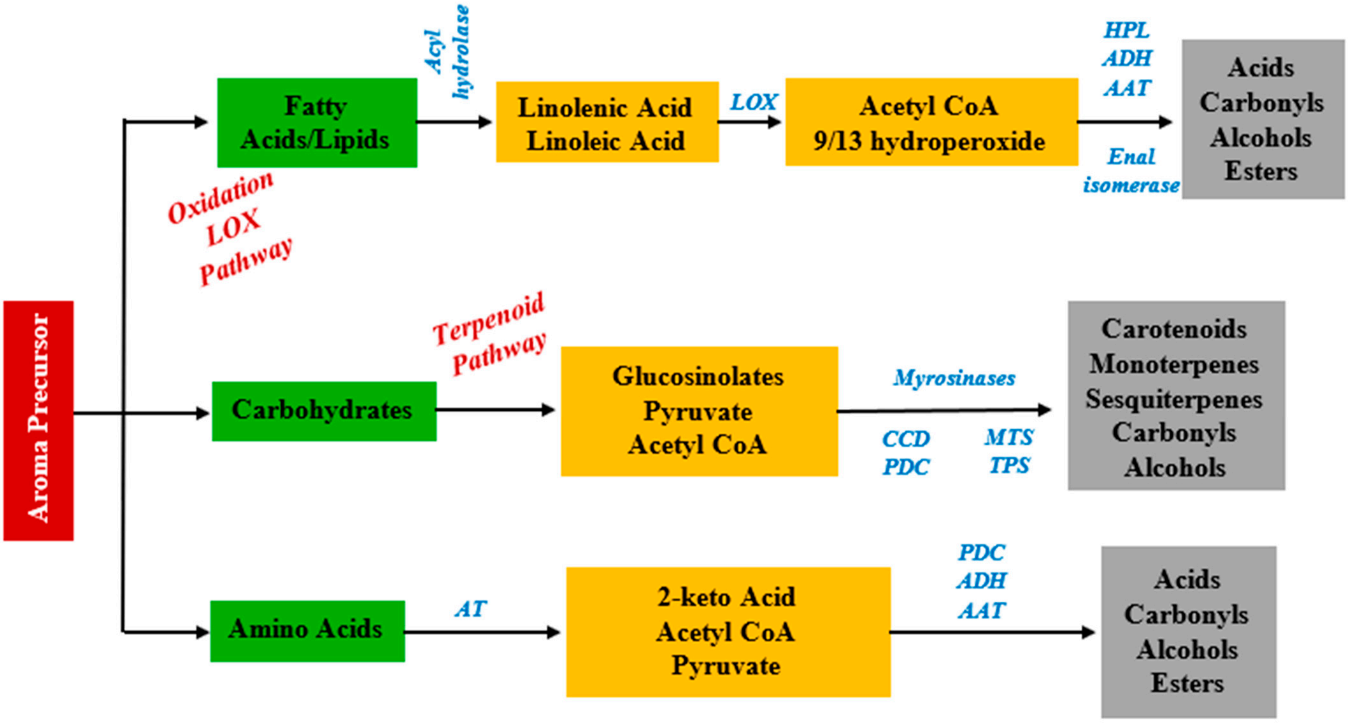

**Figure 4.** Summarized biosynthesis pathways of major aromas in grapes. Aroma precursors are highlighted in green, common pathways are italicized in red, enzymes are italicized in blue, intermediate substrates and compounds are highlighted in yellow, and volatile compounds are highlighted in gray. **LOX**, lipoxygenase; **HPL**, fatty acid hydroperoxide lyase; **ADH**, alcohol dehydrogenase; **AAT**, alcohol acyltransferase; **PDC**, pyruvate decarboxylase; **CCD**, carotenoid cleavage dioxygenase; **MTS**, monoterpene synthase; **TPS**, terpene synthase; **AT**, aminotransferase; **Acetyl CoA**, acetyl coenzyme A.

The volatile compounds of most grape varieties are similar but differ after elicitation due to modifications in the pathways. The differences are most likely associated with the genes and enzymes in the biosynthesis pathways. Elicitors may have altered the aroma-related genes, and the associated enzymes could either be activated or deactivated [136,150]. Moreover, as secondary metabolites, volatile compounds also play vital physiological roles such as resisting pests, and attracting pollinators, among others [152,153]. For instance, terpenoids take part in the defense against herbivores, pathogens, and biotic and abiotic stressors [153,154]. Since the primary function of elicitors is to induce defense mechanisms, the concentration of terpenes increases specifically in most elicitor-treated grapes, as shown in numerous studies.

## 4. Conclusions

Volatile compounds are essential components of grape and wine and contribute significantly to the quality and consumer acceptance of the product. Studies have shown the ability of elicitors to enhance grape aroma quality as well as its anti-pathogenic benefits on grapes. Chitosan is involved in many antibacterial and antifungal activities and may positively or negatively affect a grape's volatile compounds and amino acid concentrations depending on its extraction and modification methods. Methyl Jasmonate (MeJ) has the potential to increase the concentrations of volatile compounds, especially terpenes and C13-norisoprenoids, with different concentrations among grape varieties. Conversely, benzothiadiazole (BTH) is very efficient in controlling grapevine diseases and improving grape phenolic compounds but has little influence on the concentration of most volatile compounds. Nevertheless, the combined impact of MeJ and BTH enhances grape quality better than BTH only.

Regardless of the elicitor type applied, its effectiveness is greatly influenced by grape genetics, seasonal variation, and application time. Most studies used elicitors at veraison, which yielded significant increases in grape qualities compared to the controls. However, few studies applied elicitors at the ripening stage and observed better improvement in grape qualities. Therefore, studies on the optimal application time of elicitors to different grape varieties are encouraged. Further studies could also focus on the modifications in grape genes related to the synthesis of volatile compounds after elicitors application.

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