The role of signal production and transduction in induced resistance of harvested fruits and vegetables

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Abstract

Postharvest diseases are the primary reason causing postharvest loss of fruits and vegetables. Although fungicides show an effective way to control postharvest diseases, the use of fungicides is gradually being restricted due to safety, environmental pollution, and resistance development in the pathogen. Induced resistance is a new strategy to control postharvest diseases by eliciting immune activity in fruits and vegetables with exogenous physical, chemical, and biological elicitors. After being stimulated by elicitors, fruits and vegetables respond immediately against pathogens. This process is actually a continuous signal transduction, including the generation, transduction, and interaction of signal molecules. Each step of response can lead to corresponding physiological functions, and ultimately induce disease resistance by upregulating the expression of disease resistance genes and activating a variety of metabolic pathways. Signal molecules not only mediate defense response alone, but also interact with other signal transduction pathways to regulate the disease resistance response. Among various signal molecules, the second messenger (reactive oxygen species, nitric oxide, calcium ions) and plant hormones (salicylic acid, jasmonic acid, ethylene, and abscisic acid) play an important role in induced resistance. This article summarizes and reviews the research progress of induced resistance in recent years, and expounds the role of the above-mentioned signal molecules in induced resistance of harvested fruits and vegetables, and prospects for future research.

Keywords: Fruits and vegetables; induce resistance; signal molecule; production; transduction.

Introduction

Fruits and vegetables are an important part of human diet. However, postharvest loss is quite a serious issue, which has long plagued the development of the fruits and vegetables industry (Walters et al., 2013). According to the data from Food and Agriculture Organization of the United Nations (FAO), the average postharvest loss of fruits and vegetables in developed countries is about 29 per cent, while that in developing countries is as high as 38 per cent (Spadaro and Droby, 2016). Postharvest diseases, ripening and senescence, physiological disorders, and water transpiration are the main causes of postharvest loss. Among them, postharvest diseases caused by pathogen infection is the most serious cause (Terry and Joyce, 2004; Schreuder et al., 2018; Wang et al., 2021). Excepting causing postharvest loss, pathogenic fungi also accumulate mycotoxins in fruits and vegetables, resulting in potential hazard to human safety (Tang et al., 2014). Traditionally, the control of postharvest diseases has mainly depended on chemical fungicides (Petriaq et al., 2018). However, due to problems such as pesticide residues, environmental pollution, registration difficulties, and long-term use of resistant and drug-resistant strains, the use of chemical fungicides has become gradually limited (Palou et al., 2016). Therefore, it is urgent to seek safer, more efficient and environmental protection methods for postharvest disease control.
Induced resistance is a new strategy that could effectively control postharvest diseases by activating the immune ability in fruits and vegetables, thereby enhancing resistance against pathogens (Petriacq et al., 2018). Compared with traditional fungicides, induced resistance has the characteristics of broad antifungal spectrum, long duration, and will not cause the emergence of resistant strains. In addition, induced resistance can also increase the content of natural compounds for disease resistance in fruits and vegetables such as phenolics, flavonoids, lignin, and other substances (Table 1), thus effectively improving the antioxidant properties of products (Romanazzi et al., 2016a). A variety of physical, chemical, and biological treatments can induce the disease resistance of harvested fruits and vegetables. The treatment or compound that can stimulate fruits and vegetables to produce disease resistance is also known as inducer or elicitor (Walters et al., 2013; Pieterse et al., 2014). Treatments such as UV-C, ozone, and heat can significantly enhance the disease resistance of mango, kiwifruit, and banana, and reduce postharvest diseases (Vilaplana et al., 2018; Luo et al., 2019; Sripong et al., 2019). Plant hormones, polysaccharides, essential oils, organic acids, and some synthetic chemicals can also induce the disease resistance of pear, apple, grape, and litchi fruit, and some of them have been commercialized (Romanazzi et al., 2016a; Jin et al., 2019; Li et al., 2020a; María-Emma et al., 2020; Zhang et al., 2021). Antagonistic yeast and yeast cell wall extracts also showed good induced effects on postharvest diseases of citrus, tomato, and peach (Zhang X. Y. et al., 2020; Zhao et al., 2020; Chen et al., 2021). In addition, studies have shown that hexanal and Bacillus amyloliquefaciens treatments have a good control effect on the soft rot of cabbage, pepper, and lettuce caused by Erwinia carotovora and Pseudomonas fluorescens (Zhao et al., 2013; Zhang et al., 2018). The types of induced resistance in plants mainly include systemic acquired resistance (SAR) mediated by salicylic acid (SA) and induced systemic resistance (ISR) dependent on jasmonic acid (JA) and ethylene (ET). Both of them can induce broad spectrum and durable defense against pathogens. The typical mechanisms involved in induced resistance mainly include signal production and transduction, oxidative burst, accumulation of pathogenesis-related proteins, activation of energy metabolism, shikimic acid pathway, and phenylpropanoid metabolism (Shorosh et al., 2010; Lloyd et al., 2011; Ge et al., 2019), among which signal production and transduction play an important role in resistance induction.

### Role of Signal Molecules in Inducing Disease Resistance of Fruits and Vegetables

It is a continuous signal transduction process from elicitor touching fruits and vegetables of activating plants defense response. Each step of signal transduction can lead to corresponding physiological functions. The reported signal molecules mainly involve reactive oxygen species (ROS), nitric oxide (NO), calcium ion (Ca\(^{2+}\)), SA, JA, ET, and abscisic acid (ABA).

### Second Messengers Signaling Molecules

#### Reactive oxygen species

Oxidative burst is a typical reaction after treatment with elicitors, in which a large amount of ROS is generally produced in the fruits and vegetables in a short time, including superoxide anion (\(O_2^-\)), hydroxyl

| Material | Elicitor | Preharvest/Postharvest | Natural compound | Reference |
|----------|----------|------------------------|------------------|-----------|
| Apple    | Sodium nitroprusside | Postharvest | Total phenolics, flavonoids, lignin | Ge et al. (2019) |
|          | Caffeic acid     |            | Total phenolics, flavonoids, lignin | Zhang M. Y. et al. (2020) |
| Grape    | Chitosan-g-salicylic acid | Preharvest | Total phenolics | Shen and Yang (2017) |
|          | Chitosan        |            | Epigallocatechin gallate, catechin, resveratrol | Zhang Z. B. et al. (2020) |
| Banana   | Gum arabic     | Postharvest | Total phenolics, flavonoids, lignin | Alihi et al. (2018) |
|          | Nitric oxide   |            | Total phenolics, flavonoids, lignin | Hu et al. (2014) |
| Mango    | Nitric oxide   | Postharvest | Total phenolics, flavonoids, lignin, anthocyanin | Ren et al. (2020) |
| Strawberry | UV-C | Preharvest | Ceanidin, quercetin, kaempferol, ellagic acid | Xu et al. (2019) |
|          | Burkholderia contaminans | Postharvest | Total phenolics, lignin | Wang et al. (2018) |
| Muskmelon | Sodium nitroprusside | Preharvest | Total phenolics, flavonoids, lignin | Wang et al. (2020) |
|          | Oxaic acid     | Postharvest | Total phenolics, flavonoids, lignin | Deng J. et al. (2015) |
| Tomato   | Hot air        | Postharvest | Caffeic acid, p-coumaric acid, chlorogenic acid, quercetin, rutin | Wei et al. (2017) |
| Cirtu    | Oligochitosan  | Postharvest | Total phenolics, flavonoids, lignin | Deng L. L. et al. (2015) |
|          | Nitric oxide   |            | Total phenolics | Zhou et al. (2016) |
| Peach    | Pichia membranefaciens | Postharvest | Flavonoids, lignin | Zhang X. Y. et al. (2020) |
|          | Methyl jasmonate |            | Chlorogenic acid, neochlorogenic acid, epicatechin | Ji et al. (2021) |
| Jujube   | Salicylic acid | Postharvest | Caffeic acid, p-coumaric acid, catechin, epicatechin, rutin | Yuan et al. (2019) |
| Kiwifruit | Chitosan and sodium silicate | Postharvest | Total phenolics, flavonoids, lignin | Guo et al. (2019) |
|          | Sodium nitroprusside |            | Total phenolics, flavonoids, lignin | Zhang et al. (2017) |
|          | Methyl jasmonate |            | Total phenolics | Pan et al. (2019) |
| Litchi   | Melatonin     | Postharvest | Total phenolics, flavonoids, lignin | Zhang et al. (2021) |
|          | Bacillus amyloliquefaciens |            | Lignin | Wu et al. (2017) |
radical (–OH), and hydrogen peroxide (H₂O₂; Mittler, 2017). As a signal molecule, ROS can activate redox-dependent transcription factors, activate the expression of defense genes, and induce resistance against pathogens (Huang et al., 2019). After treatment with elicitors, Ca²⁺-ATPase is first induced, leading to Ca²⁺ influx, which activates calcium-dependent protein kinase (CDPK). CDPK phosphorylates NADPH oxidase (NOX) and forms O₂⁻ by electron transfer. Due to the short half-life, O₂⁻ is disproportionated to H₂O₂ under the action of superoxide dismutase (SOD; Jeandroz et al., 2013). As a signal molecule, ROS can regulate the key regulator NPR1 in SAR, and induce the expression of defense genes such as glutathione-S-transferase and glutathione peroxidase (Mou et al., 2003). This result showed that chitosan treatment induced resistance against Penicillium italicum and Penicillium digitatum (P. digitatum) in navel orange fruits by promoting the accumulation of H₂O₂ (Zeng et al., 2010). Acibenzolar-S-methyl (ASM) treatment enhanced the resistance of apple to Penicillium expansum (P. expansum) by increasing the activity of NOX and SOD and promoting the accumulation of H₂O₂ (Botrytis cinerea (B. cinerea); Wei et al., 2019). Melatonin treatment significantly increased the content of H₂O₂ in tomatoes, thereby enhancing the resistance of fruit against B. cinerea (Liu et al., 2019). In addition, acidic electrolyzed water treatment also significantly accelerated the accumulation of H₂O₂, which enhanced the resistance of longan against Phomopsis longanae and Lasiodiplodia theobromae (Tang et al., 2020). These results show that ROS are involved in induced disease resistance of harvested fruits and vegetables by elicitors.

Nitric oxide

NO is an important signaling molecule, which is involved in the regulation of multiple physiological processes. NO could mediate plants’ defense response to pathogens by stimulating resistance-related programmed cell death and inducing the expression of defense genes (Domingos et al., 2015). Nitrate reductase (NR), nitric oxide synthase (NOS) and inorganic nitrogen pathways are the main sources of NO synthesis in plants. Among them, NR and NOS have been proved to be the key enzymes for the production of NO when plants respond to stress (Yamamoto et al., 2003; Crawford and Guo, 2003; Zheng et al., 2011). Like ROS, NO burst is a typical feature after the elicitor treatment of plants. The signal transduction of NO in induced resistance mainly occurs through two pathways. One is the cyclic guanosine monophosphate (cGMP) signaling pathway, which increases the level of NO by activating NOS, which binds with soluble guanylate cyclase, which activates cGMP-dependent protein kinase and increases the concentration of cyclic adenosine diphasphate ribose (cADPR). cADPR kinase increases the concentration of Ca²⁺ and induces the expression of resistance genes such as PR-1 (Klessig et al., 2000). The other pathway is independent of the cGMP signaling pathway. NO can also participate in disease resistance by inhibiting the activity of aconitase. NO directly regulates the activity of effector proteins by posttranscriptional modification of target proteins, or induces the production of SA and ROS by increasing the second messengers such as cGMP and Ca²⁺ level, thereby enhancing the resistance (Domingos et al., 2015). The treatment of B. cinerea culture medium extract resulted in a large amount of NO production in tomato, which significantly induced the resistance of fruit against B. cinerea. However, treatment with N-nitro-L-arginine (L-NNA), a NOS inhibitor, inhibited the disease resistance of tomato induced by B. cinerea extract by blocking the production of NO (Zheng et al., 2011). Arginine treatment significantly promoted the accumulation of NO in strawberry by triggering the activity of NOS, and enhanced the resistance of fruits against B. cinerea. L-NNA treatment weakened the disease resistance induced by arginine, leading to more serious fruit rot (Shu et al., 2020). Yeast saccharide treatment increased the endogenous NO level in peach and enhanced the resistance of fruit against P. expansum. However, treatment with the specific NO scavenger 2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide (c-PTIO) attenuated the disease resistance of peach induced by Yeast saccharide by removing the endogenous NO (Yu et al., 2012). In addition, methyl jasmonate (MeJA) treatment enhanced the resistance of blueberry against B. cinerea by inducing rapid accumulation of endogenous NO (Wang et al., 2020). These results indicate that NO is involved in induced disease resistance of harvested fruits and vegetables by elicitors.

Calcium ion

Ca²⁺ is widely involved in the induction of disease resistance through changes in enzymes activity that depend on Ca²⁺ and calcium binding proteins (such as calmodulin (CaM); Li and Zou, 2016; Wang et al., 2016). Under normal conditions, the cytoplasmic Ca²⁺ concentration is maintained at a relatively low inactive state, while the concentration of Ca²⁺ in the cell wall (extracellular Ca²⁺) and calcium pool (such as vacuole, nucleus, endoplasmic reticulum, chloroplast, and mitochondria; intracellular Ca²⁺) is much higher than that in the cytoplasm (Knight, 2000; White, 2000). When cells are stimulated, Ca²⁺ extracellular and intracellular calcium pools flows into the cytoplasm through the calcium channels on the plasma membrane and releases to the cytoplasm through the calcium channels on the organelle membrane, respectively, causing a significant increase in the concentration of Ca²⁺ in the cytoplasm and producing calcium signals (Reddy, 2001). The increase of Ca²⁺ concentration activates calcium binding proteins such as calmodulin, CDPKs and downstream calcium-regulated transcription factor crazy1 (Crz1), thereby mediating cell defense response (Ning et al., 2019). Exogenous NO treatment significantly enhanced the resistance of peach against Monilinia fructicola by increasing Ca²⁺ concentration (Shi et al., 2015). Calcium chloride treatment enhanced the resistance of melons against Penicillium by upregulating the expression of HmCDPK2 and increasing the activity of CDPK (Ning et al., 2019). In addition, calcium chloride treatment also induced the resistance of tomato against B. cinerea by promoting ROS accumulation (Li and Zou, 2016). These results indicate that Ca²⁺ also plays an important role in induced resistance of harvested fruits and vegetables by elicitors.

Hormone Signaling Molecules

Salicylic acid

As a plant hormone, SA is widely involved in signal transduction in induced resistance of fruits and vegetables (Romanazzi et al., 2016a; Wang et al., 2019). SA and its SA analogues benzo[1,2-c:4,5-c′]diazole and 2,6-dichloroisonicotinic acid can induce SAR production in plants. SA is synthesized by two pathways starting from chorismic acid, one is the isochorismic acid synthase (ICS) pathway, which is the main pathway for SA synthesis in activating plants’ defense response; the other is phenylpropanoid metabolism (Hao et al., 2018). SA catalyzes the conversion of transcription factor NPR1 from a polymer to a monomer by activating thioredoxin, and transfers from the cytoplasm to the nucleus. Then, NPR1 interacts with TGACGTCA cis-element-binding protein (TGA) to regulate the expression of downstream defense genes (such as the PR gene; Kumar, 2014;
Zhang J. J. et al., 2019). Therefore, nonexpressor of pathogenesis-related genes1 (NPR1) is considered to be the master regulator of SAR located downstream of SA, which regulates and induces SAR by interacting with transcription factors such as TGA (Ekengren et al., 2003). It was reported that melatonin and chitosan treatment significantly increased the endogenous SA level and enhanced the resistance of tomato and grapefruit against *B. cinerea* and *P. digitatum* (Shi et al., 2018; Li et al., 2019). Antagonistic yeast, Cryptococcus laurentii (*C. laurentii*), treatment also significantly enhanced the resistance of tomato to *B. cinerea* and *Alternaria alternate* by activating the SA signal transduction pathway (Lai et al., 2018). Chlorogenic acid and chitin from cell wall extract of Saccharomyces cerevisiae induced the resistance of peach and tomato against *P. expansum* and *B. cinerea* by upregulating the expression of ICS and phenylpropanoid ammonia lyase (Jiao et al., 2018; Sun et al., 2018). These results suggest that SA plays an important role in induced resistance of harvested fruits and vegetables by elicitors.

**Jasmonic acid**

JA and its volatile ester derivative MeJA are a class of growth regulators widely existing in plants, which act as signal molecules to induce defense gene expression and enhance the resistance of plants to biotic and abiotic stresses (Ruan et al., 2019). JA is synthesized by ω-linolenic acid via lipoxygenase pathway (Carvalhais et al., 2017). When plants are stimulated by elicitors, JA is rapidly synthesized in cells, and the synthesized JA combines with isoleucine to produce active JA-Ile. JA-Ile interacts with the receptor proteins COH1 and JAZ to form a complex, and then degrades the ubiquitinated JAZ protein through the 26S proteasome. Because the JAZ protein can inhibit the activity of the transcription factor MYC2, when JAZ is decomposed, the transcription factor MYC2 is released, activating the JA signaling pathway, thus inducing systemic resistance (Chico et al., 2008; Zamioudis and Pieterse, 2012; Carvalhais et al., 2017). Sodium nitroprusside and melatonin treatment significantly increased endogenous JA and MeJA content in peach and tomato, and enhanced the resistance of fruit against Monilinia fructicola and *B. cinerea* (Shi et al., 2015; Liu et al., 2019). Antagonistic yeast Pichia membranefaciens also enhanced the resistance of peach against Rhizopus oryzae by upregulating the expression of transcription factors MYC and MYB in the JA signaling pathway (Zhang X. Y. et al., 2020). In addition, the ephelton treatment weakened the resistance of banana fruit to Colletotrichum musae by inhibiting JA biosynthesis (Zhu et al., 2011). These results indicate that the disease resistance of fruits and vegetables induced by elicitor treatment was closely related to endogenous JA level.

**Ethylene**

Ethylene is the gaseous hormone in plants, which not only regulates the growth and development of plants, but also is a key regulator for plants to cope with biological stress (Chen et al., 2005; Mengiste, 2012; Larsen, 2015). The biosynthesis of ET mainly occurs during ripening, senescence, or stress. The production of ET induced by stress is also called stress ET and plays an important role in disease resistance (Megías et al., 2013; Wang et al., 2019). Methionine is the precursor of ET biosynthesis, which is converted to S-adenosylmethionine (SAM) by S-adenosylmethionine synthase, and SAM is converted to 1-aminocyclopropane-1-carboxyl acid (ACC) by 1-aminocyclopropane-1-carboxylic acid synthase (ACS). Subsequently, ACC is oxidized to produce ET by ACC oxidase (ACO; Jennifer et al., 2006; leendert et al., 2006). ACS and ACO are the key enzymes in the ET biosynthetic pathway (Lee et al., 2017). After binding with ET, the ET receptor can inhibit the activity of the negative regulator CTR1, activate the positive regulator EIN2, transfer its C-terminal to the nucleus, and transmit the signal to the transcription factor EIN3/EIL to activate the downstream ET response gene ERF, thus activating ethylene-mediated defense response. Sodium nitroprusside, melatonin, and heat treatment inhibited ET synthesis in mangoes, apples, and bamboo shoots by inhibiting the activity of ACS (Luo et al., 2012; Deng et al., 2013; Liu et al., 2020). Antagonistic yeast *C. laurentii* treatment increased the ET level of tomato and enhanced the resistance of tomato against *B. cinerea* (Tang et al., 2019). Acremonium strictum Ellicitor Suberin (AsES) treatment also significantly promoted the accumulation of ET in avocado and enhanced the resistance of fruit against Lasiodiplodia theobromae, while treatment with the ET receptor blocker 1-MCP weakened the resistance of avocados induced by AsES (Perato et al., 2018). MeJA treatment promoted the synthesis of ET in tomato fruits by increasing the activity of ACO, and significantly enhanced the resistance of fruit against *B. cinerea* (Yu et al., 2009). In addition, heat treatment can also increase the expression of the ACO gene and enhance the resistance of banana against Colletotrichum gloeosporioides (*C. gloeosporioides*) (Zhu et al., 2011). These results indicate that ET is involved in disease resistance of harvested fruits and vegetables induced by elicitors.

**Abscisic acid**

As a plant hormone, ABA plays an important role in inducing stomatal closure, promoting growth and development, regulating fruit ripening and senescence, and responding to biotic and abiotic stresses (Cao et al., 2019). There are direct and indirect pathways for ABA synthesis in plants, of which the indirect pathway from carotenoid oxidative decomposition is the main one (Yang et al., 2015). Carotenoids are first cracked into xanthoxin (XAN), the precursor of C15, and XAN is further converted into abscisic aldehyde. Finally, the biologically active ABA is generated under the action of abscisic aldehyde oxidase (Nambara and Marion-Poll, 2005). ABA in plants contains two signal transduction pathways, ABA independent and ABA dependent. In the ABA-independent pathway, the presence and expression of ABA are not necessary for the occurrence of the signal pathway. Proteinphosphatase 2C combines with SnRK2 kinase to dephosphorylate the latter, thus losing its activity (Park et al., 2009). In the ABA-dependent pathway, ABA forms a complex with its protein receptor, and then binds with PP2C to break the binding between proteinphosphatase 2C and SnRK2, so that SnRK2 can restore phosphorylation and regain activity, thus activating downstream transcription factors, inducing downstream gene expression, and regulating plant disease resistance (Hauser et al., 2011). Treatment with antagonistic fungus Clonostachys rosea reduced the endogenous ABA levels of tomato and enhanced the resistance of fruit against *B. cinerea* (Gong et al., 2017). Chitosan treatment reduced the content of ABA in mango peel and enhanced the resistance of mango against *C. gloeosporioides* (Limon et al., 2020). The resistance of tomato mutants with low endogenous ABA level to *B. cinerea* was significantly lower than that of wild type (Audenaert et al., 2002). Exogenous ABA treatment promoted the accumulation of endogenous ABA and reduced the resistance of Arabidopsis thaliana to Pseudomonas syringae (Fan et al., 2009). Exogenous ABA could significantly increase the expression of resistance genes such as PR1 and GLU in tomato, and enhance the resistance to Alternaria solani (Song et al., 2011). These results indicate that the level of ABA is closely related to the resistance of fruits and vegetables induced by elicitors.
Conclusion and Future Prospects

The above results indicated that ROS, NO, SA, Ca$^{2+}$, JA, ET, and ABA were involved in the disease resistance of harvested fruits and vegetables induced by elicitors. However, the current research mainly focuses on the production of a single signal molecule, and there is a lack of information on the production of multiple signal molecules. Studies have shown that *Clusia rosea* significantly increases the content of SA and NO during the process of inducing disease resistance in tomato, but inhibits the production of ABA (Gong et al., 2017). When the ROS level in grape was low, NO could induce ROS production. However, when ROS was overaccumulated, NO could reduce the ROS level by increasing the activity of antioxidant enzymes (Zhang Z. et al., 2019). In addition, the increase of endogenous NO levels in peach could also induce the increase of SA and JA contents and Ca$^{2+}$ concentration (Shi et al., 2015). These results indicated that a variety of signal molecules are involved in the induced resistance of harvested fruits and vegetables. Although there are lots of studies on the generation and transduction of signal molecules in induced resistance, most focus on model plants (Mishra et al., 2012; Xiang et al., 2020). Most of the existing reports of harvested fruits and vegetables treated with elicitors are focused on the production of signal molecules, and the production process and species of signal molecules are basically the same as model plants (Niko and Silke, 2008; Mauch-Mani et al., 2017; Wang et al., 2019). Based on the above point of view, we speculated the possible interaction mechanism of signal molecules in induced resistance of harvested fruits and vegetables (Figure 1). After elicitor treatment of fruits and vegetables, it first promotes a Ca$^{2+}$ influx and induces ROS production. Because ROS has a strong regulatory effect on Ca$^{2+}$ channels and Ca$^{2+}$ concentration, when ROS accumulates to a certain level, it could in turn promote Ca$^{2+}$ influx, thereby inducing an oxygen burst (Jeandroz et al., 2013; Ning et al., 2019). At the same time, the SA synthesis pathway is activated, which cooperates with ROS to mediate SAR and participate in the defense response (Shoresh et al., 2010; Shi et al., 2015). SA can also bind to the SA binding protein and induce ROS accumulation by inhibiting catalase activity. The synergistic effect between ROS and NO is crucial for the full activation of the defense response, and they regulate the accumulation of each other in cells (Floryszak and Arasimowicz, 2016; Igor et al., 2019). ISR is mediated by JA and ET, which can also induce ROS accumulation (Romanazzi et al., 2016a). In addition, NO can also inhibit the biosynthesis of ET (Hu et al., 2014).

Although induced resistance shows advantages and broad development prospects, the challenge remains concerning its application in agriculture. Some elicitors are difficult to realize commercial application due to the high cost of review and registration (Romanazzi et al., 2016a), and induced resistance is not as effective as fungicides (Thakur et al., 2013). Therefore, the mixed use of elicitors and fungicides not only minimize the use of chemical fungicides, but also effectively ensure the control of postharvest diseases (Romanazzi et al., 2016b). Preharvest treatments have gained increasing attention in recent years owing to certain characteristics such as simplicity, efficiency, and safety (Martinez-Esplá et al., 2019; Wang et al., 2021). Compared with the postharvest treatment, which involves complete exposure, preharvest sprays not only affect the fruit, but also other portions of the plants, which could indirectly affect fruit quality (Xu et al., 2019). In addition, the fruits and vegetables are more sensitive to induced resistance during development (Zhang et al., 2011). Therefore, we suggest that preharvest treatment is more effective than postharvest treatment. At the same time, the screening of new elicitors is also very important. In recent years, some biological control agents have gradually been widely used due to their good disease control effects. Data show that the global (2012–2020) market growth rate of biologics has reached 12.3 per cent per year, while the growth rate of chemical pesticides is only 5 per cent (Droby et al., 2016). However, the optimal concentration and times of application of elicitors on different fruits need to be further determined.

By and large, there are few reports about the role of signal transduction in induced resistance of fruits and vegetables by elicitors, and most of the existing studies come from model plants. Due to the different response patterns to different types of elicitors and pathogens in fruits and vegetables, the conduction network is complex. However, what is exciting is that the research level of some promising emerging technologies such as molecular biology and omics have made great progress in the past decade. Therefore, we believe that in the near future, the mechanism and unknown functions of signal molecules in induced resistance, such as spatial order, signal transduction pathway and interaction, interaction between signal molecules and transcription factors and resistance genes, will be further revealed.

**Figure 1.** Possible interaction mechanism of different signaling molecules in induced resistance of harvested fruits and vegetables by elicitors. Elicitor treatment induces the production and accumulation of signaling molecules such as ROS, NO, Ca$^{2+}$, SA and JA by activating different metabolic pathways (yellow arrow). Different signal molecules interact with each other and participate in induced resistance (green arrow indicates promotion and the red line indicates inhibition). ABA, abscisic acid; Ca$^{2+}$, calcium ion; ET, ethylene; ISC, isochorismic acid synthase; ISR, induced systemic resistance; JA, jasmonic acid; LOX, lipoxygenase; NO, nitric oxide; NOS, nitric oxide synthase; NOX, NADPH oxidase; NR, nitrate reductase; PAL, phenylpropanine ammonia lyase; ROS, reactive oxygen species; SA, salicylic acid; SAR, systemic acquired resistance.

**Author Contributions**

Bin Wang contributed to conceptualization, writing-original draft preparation, software, writing-reviewing and editing. Yang Bi contributed to conceptualization, writing-original draft preparation, supervision.

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Conflict of Interest
The authors declare no conflict of interest.

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