



Review **Recent Advances in Mechanisms Underlying Defense Responses of Horticultural Crops to** *Botrytis cinerea*

Rui Li and Yulin Cheng *

Key Laboratory of Plant Hormones and Development Regulation of Chongqing, School of Life Sciences, Chongqing University, Chongqing 401331, China; 20222601002@stu.cqu.edu.cn * Correspondence: yulincheng@cqu.edu.cn

Abstract: Horticultural crops are a crucial component of agriculture worldwide and have great economic value. The notorious plant fungal pathogen Botrytis cinerea can cause gray mold disease in over 200 horticultural crops, leading to severe economic losses. Investigating the mechanisms underlying plant defense responses to pathogens is crucial for developing new strategies for effectively controlling plant diseases, and much progress has occurred in the mechanisms underlying defense responses of horticultural crops to B. cinerea mainly due to the completion of genome sequencing and the establishment of efficient tools for functional genomics. In this review, recent progress in mechanisms underlying defense responses and natural products that can enhance the resistance of horticultural crops to B. cinerea are summarized, and future research directions are also discussed.

Keywords: Botrytis cinerea; plant defense responses; pattern-triggered immunity; hormone; disease control

1. Introduction

Horticultural crops include fruits, vegetables, and ornamental plants, containing enormous nutritional and ornamental value. Production and consumption of horticultural products are developing rapidly, thereby attracting much attention [1]. However, horticultural crops are seriously threatened by various pathogens in the field, transport, storage, and even market [2]. B. cinerea, the second most important fungal plant pathogen, can cause gray mold disease in over 200 horticultural crops, such as tomato, strawberry, grape, and rose, resulting in severe economic losses [3,4]. Health or environmental risks derived from synthetic fungicides and fungicide resistance are increasingly concerning [5,6]. Thus, it is imperative to develop new strategies for effectively controlling gray mold disease.

During pathogen–plant interactions, plants have evolved unique disease resistance mechanisms and strategies to deal with pathogens to reduce the damage [7]. With the development of genome sequencing [8], and the establishment of efficient tools for functional genomics [9], there have been numerous important advances in our understanding of the molecular biology of members in plant defense response to pathogens. Pattern-triggered immunity (PTI) is a key component of plant immune responses to B. cinerea [10], and components in plant PTI signaling, transcription factors, and proteins in hormone synthesis and signaling were proven to be important regulators against *B. cinerea* infection [11]. This article reviews the research progress on defense response mechanisms of horticultural crops and natural products that enhance resistance to *B. cinerea* in recent years, and prospects for future research directions.

2. Physiological Responses to B. cinerea in Horticultural Crops

2.1. Increase in the Production of Reactive Oxygen Species (ROS) and Nitric Oxide (NO)

The so-called reactive oxygen species (ROS) include various forms of reducing and chemically reactive molecules such as superoxide anion, hydrogen peroxide, hydroxyl radical, or hydroperoxyl group. The outbreak of ROS is one of the main immune responses of



Citation: Li, R.; Cheng, Y. Recent Advances in Mechanisms Underlying Defense Responses of Horticultural Crops to Botrutis cinerea. Horticulturae 2023, 9, 1178. https://doi.org/ 10.3390/horticulturae9111178

Academic Editors: Loredana Sigillo and Eliana Dell'olmo

Received: 14 September 2023 Revised: 24 October 2023 Accepted: 26 October 2023 Published: 27 October 2023



Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/).

plants to resist the invasion of pathogens [12]. Oxygen acts as a signaling molecule, and the production of reactive oxygen species can serve as a marker for the successful identification of infection and activation of plant defense (Figure 1). The infection of *B. cinerea* caused changes in the activities of superoxide dismutase (SOD) enzymes, ascorbate peroxidase, flavonoid peroxidase, catalase, and other antioxidant enzymes in apple fruit [13]. Furthermore, some other crops also showed varying degrees of change, for instance, the activities of three antioxidant enzymes SOD, peroxidase (POD), and catalase (CAT)) in infected grape berries were improved to different degrees [14], and the content of H_2O_2 and O_2^- as well as the activity of SOD, POD, and CAT were influenced in infected cucumber [15]. These situations indicate that modifying ROS homeostasis by altering the regulatory components of ROS production in plant immunity contributes to engineering or breeding broad-spectrum disease-resistant crops [16].



Figure 1. Immune responses against *B. cinerea* in tomato. Chitin, other pathogen-associated molecular patterns (PAMPs), and phytosulfokin (PSK) are recognized by receptor-like proteins and kinases that serve as PRRs. SILYK4 interacts with SICERK1, which recognizes chitin from *B. cinerea*. SIRIPK influences downstream ROS, while SIPSKR1 recognizes PSK, but how it works remains unclear. The activation of MAPK cascade is an important component of PTI signaling. Several major classes of transcription factors (TFs), mainly including WRKYs, ERFs, MYBs, bHLHs, and NACs, were implicated in immune responses to *B. cinerea* and may be targets of MAPK phosphorylation. These TFs influence the level of plant defense hormones by modulating gene expression. Mediator is an evolutionarily conserved multisubunit complex that regulates the function of RNA merase. Tomato mediator complex SIMED8 and SIMED25 contribute to immune responses to *B. cinerea* by modulating gene expression. Some other genes in the cytoplasm also affect the metabolites and phytohormones signaling.

Nitric oxide (NO) also plays a key role in different physiological processes of plants (Figure 1). The production of NO usually involves two main pathways: the NR pathway, reducing nitrite to NO; and the oxidation pathway of nitric oxide synthase (NOS) [17]. The

accumulation of nitric oxide in tomatoes increased resistance to *B. cinerea* [18,19]. Higher NO supply resulted in much metabolism in tomatoes, which led to higher resistance against *B. cinerea* [20]. NO accumulated in tomato chloroplasts [21] and the level of NO influenced the activities of phenylalanine ammonia-lyase (PAL), chitinase (CHI), β -1, 3-glucanase (GLU), and polyphenol oxidase (PPO) [19,22,23], while the accumulation of H₂O₂ decreased [24], which eventually improved the resistance against *B. cinerea*. In potato leaves, *B. cinerea* induces massive accumulation of nitric oxide and H₂O₂ and ultimately induces programmed cell death [25]. Generally, NO can induce ROS production and enhance ROS-related enzymatic activities [26,27].

2.2. Change in Plant Metabolites

A large number of plant metabolites including primary metabolites and secondary metabolites (Figure 1) are involved in the process of plant disease resistance. Several processes involved in the metabolism of amino acids and carbohydrates were triggered by B. cinerea in grape berries, and a large number of peptides, fatty acids, hydroxy fatty acids, glycerophospholipids, and glycosphingolipids were accumulated [28]. Other aromatic compounds, including acetophenones, benzoic acid derivatives, methoxyphenols, and phenolic glycosides, showed increased abundance upon *B. cinerea* infection [28]. The content of vitamin C and phenolic substances, which are two antioxidant metabolites, was increased in the apple fruit epidermis upon *B. cinerea* infection [13]. When the tomato was treated with B. cinerea, glycolysis products were reduced and TCA intermediates as well as short-chain fatty acids caproic acid and its derivatives were increased. Significantly, the content of tryptophan and shikimic acid has changed [29]. The glucosinolate biosynthesis pathway is involved in many plant defense responses to pathogens, and a study in roses showed that key metabolites of the glucosinolate biosynthesis pathway, including L-valine, L-isoleucine, and L-leucine, were altered upon B. cinerea infection [30]. B. cinerea-infected strawberries were found to show increased content of hexadecanoic acid, octadecanoic acid, sucrose, and β -lyxopyranose [31]. Overall, different plant species showed various accumulations of metabolites upon *B. cinerea* infection [32], and the change in plant metabolites is an important plant response to B. cinerea.

3. Regulators of Disease Resistance to B. cinerea in Horticultural Crops

3.1. Components of Plant PTI Signaling

3.1.1. Receptor-like Kinases

The pattern is generally specific to pathogenic microorganisms and pathogen-related molecular patterns (PAMPs) are one of the patterns. The recognition of PAMPs depends on the pattern recognition receptors (PRRs) on the surface of plant cells (Figure 1). Generally, pattern recognition receptors can be divided into receptor-like kinases (RLKs) containing kinase regions and receptor-like proteins (RLPs) which have no kinase region. The receptor for chitin recognition in tomato is LYK [33], and SlLYK4 and SlCERK1 mediate tomato resistance to *B. cinerea* [34]. Meanwhile, TPK1 complexes with SlLYK1 to recognize chitin, which implies that these PRRs may be involved in chitin-induced immunity. Receptor-like kinases SlPSKR1 in tomato conferred resistance to *B. cinerea* [35]. In addition, wall-associated kinase (WAK)/WAK-like (WAKL) is one of the subfamilies of kinase (RLK) receptors, and a total of 68 RcWAK/RcWAKL gene family members were identified in the rose genome, among which RcWAK4 [36], RcWAK8, and RcWAK22 [37] were involved in plant resistance to *B. cinerea*.

3.1.2. Receptor-like Cytoplasmic Kinases

The receptor-like cytoplasmic kinases (RLCKs)—with no extracellular domain and no transmembrane helix, but only the cytosolic kinase domain—also have an important role in triggering PTI immune responses [38]. Typically, RLCKs are phosphorylated by PRRs, which in turn activate their immune functions that induce downstream immune signals [39]. Overexpression of receptor-like cytoplasmic kinase SIRIPK confers broad-spectrum disease

resistance without a yield penalty in tomato plants. Although few RLCKs have been reported, some results indicate that RLCK has played an important role in defense response to *B. cinerea*.

3.1.3. Mitogen-Activated Protein Kinase (MAPK) Cascade

MAPK cascade is a conserved signal transduction module that can convert in vitro signals into in vivo signals [40]. Mitogen-activated protein kinases (MAPKs) are key signaling regulators of PTI [41]. MAPK cascades mainly include three types of protein kinases, including MAPKKK, MAPKK, and MAPK. It is the way to further transmit and expand these signals [40] (Figure 1 and Table 1). In tomato, SIMKK2 and SIMKK4 positively regulate the resistance response, but the specific action pathway is not yet clear [42]. Inhibition of SIMPK1/2/3 disrupted defense signaling pathways and enhanced the susceptibility to *B. cinerea* [43]. For instance, SIMAPK3 plays a positive role in the defense response by regulating the accumulation of ROS and the SA/JA pathway [44]. In addition, treatment of MAPK inhibitor reduced tomato resistance to B. cinerea and overexpression of LeMAPK1, LeMAPK2, and LeMAPK3 increased tomato resistance to B. cinerea [45], which implies that MAPK is crucial for tomato resistance to B. cinerea. Other crop species also showed similar results, for example, potato StMKK1 improved plant resistance to B. cinerea by regulating PTI responses and salicylic acid-related signaling pathways [46]. Strawberry FaMAPK5 and FaMAPK10 regulated plant resistance to *B. cinerea* mainly by regulating the content of abscisic acid (ABA) and ROS as well as the enzymatic activities of related enzymes [47]. Strawberry FaMAPK19 has also participated in plant resistance to B. cinerea, but how it works remains unclear [48]. In conclusion, the MAPK cascade also plays an important role in defense response to B. cinerea.

3.2. Transcription Factors

Transcription factors (TFs), also known as trans-acting factors, refer to DNA-binding proteins that can specifically interact with *cis*-acting elements of eukaryotic genes to activate or inhibit gene transcription. TFs play an important regulatory role in disease resistance to *B. cinerea* in horticultural crops [49] (Figure 1 and Table 1).

3.2.1. WRKY Transcription Factors

WRKY transcription factors are a large family that responds to biological stress. Tomato SIDRW1 has two WRKY domains and belongs to the WRKY family Group I; its expression was induced by *B. cinerea* and increased plant resistance to *B. cinerea* [50]. Strawberry WRKY11 influences the expression of other TFs such as WRKY1, WRKY70, and MYB1, and then positively regulates plant resistance to *B. cinerea* [51]. Other WRKY transcription factors including WRKY10 in cucumber and grapevine [15], WRKY25 [52] and WRKY50 [53] in strawberry, WRKY31 [54] and WRKY46 in tomato [55], and rose WRKY41 [56] were also reported to improve resistance to *B. cinerea*, while Lily WRKY39 and WRKY41a [57] have negative roles in plant resistance to *B. cinerea*. In addition, rose WRKY13 promoted resistance to *B. cinerea* by enhancing cytokinin content and reducing abscisic acid signaling [58].

3.2.2. MYB Transcription Factors

MYB family transcription factor is one of the largest transcription factors in plants [59]. It refers to a class of transcription factors containing the MYB domain. The MYB domain is a peptide segment of about 51–52 amino acids. Similarly, the MYB transcription factor can pass different pathways to regulate disease resistance responses [60]. MYB transcription factors are generally involved in plant resistance to *B. cinerea* by mediating the JA defense pathway, such as rose MYB84 and MYB123, which have opposite functions [61]. Tomato SIMYB75 increased the accumulation of JA and activated the JA defense signaling pathway upon *B. cinerea* infection [62]. Tomato SIMYB1 binds to the promoters of lycopene synthesis-related genes (*SILCY1* and *SIPSY2*) and the pathogen-related gene *SIPR5* to regulate lycopene production and plant resistance to *B. cinerea* [63]. VvMYB44 directly

activated the transcripts of enzyme-encoding genes involved in phenylpropanoid and sucrose metabolism [64]. MYB1, MYB10, MYB44.2, and MYB44.3 in strawberries were also involved in plant resistance to *B. cinerea* [48].

3.2.3. bHLH Transcription Factors

Basic helix-loop-helix proteins (bHLHs) are also one of the largest transcription factor families and have a basic region and an HLH (helix-loop-helix) region [64,65]. SIJIG belongs to the bHLH family and participated in tomato resistance to *B. cinerea* [66]. Rose RcbHLH13, RcbHLH35, RcbHLH41, RcbHLH44, and RcbHLH49 were upregulated after *B. cinerea* treatment, which indicates that these bHLHs may be engaged in alleviating biotic stress [67]. As a subfamily of bHLH TFs, tomato SIMYC2 plays an important role in methyl-jasmonate-induced fruit resistance to *B. cinerea* [68].

3.2.4. NAC Transcription Factors

NAC transcription factors are a type of transcription factor that is unique to plants, and there are over 100 NAC transcription factors in plants. Tomato SISRN1 has a typical NAC domain and affects the amount of ROS and resistance to *B. cinerea* by affecting superoxide dismutase and catalase [69]. Moreover, grapevine VvNAC1 is a crucial regulatory component of the plant signaling defense cascade [70].

3.3. Proteins in Hormone Synthesis and Signaling

Plant hormones are an important signal transduction pathway in plant disease resistance. Salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) play a major role in this process; at the same time, regulators such as gibberellins (GAs), auxin (AUX), and ABA also participate in this process [58,71–74]. Plant hormones can not only interact with each other but can also be involved in multiple resistance reactions [75] (Figure 1).

3.3.1. Jasmonic Acid

JA is generally involved in the resistance response to necrotic pathogens and is a class of endogenous signaling molecules of hydroxyl lipids [76]. JA is synthesized in plastids, peroxisomes, and cytoplasm, and enzymes involved in JA synthesis mainly include LOX, AOS, and AOC [77]. JA synthesis genes affected crops resistance to B. cinerea [78,79]. Tomato SITD2 is a threenine deaminase that converts threenine to α -ketobutyrate and ammonia as the committed step in isoleucine (Ile) biosynthesis and contributes to JA responses by producing the Ile needed to make the bioactive JA–Ile conjugate [80]. SIBBX20 attenuates JA signaling and regulates resistance to *B. cinerea* in tomato [81]. Methyl jasmonic acid and isoleucine jasmonic acid are derivatives of JA and play important roles in plants. COI1 is a receptor for jasmonic acid [82] and normally forms a complex with SCF ubiquitination enzymes, so the changes of these major genes influence the production of JA. JA influences multiple processes including ROS, resistance genes, and disease resistance enzymes. Extensive research has established that ROS is the most notable change in the JA pathway [55,83,84]. Extensive research in different plant species and various biological situations has revealed that there might be different expression levels of downstream genes. For example, these PR family genes including PR1, PR2a, PR2b, PR3a, and PR3b were reduced in the tomato slarg2 mutants [85]. Overexpression of VvCOI1 in strawberry fruit resulted in upregulation of the expression levels of a series of plant defense-related genes, such as PAL gene, superoxide dismutase (SOD) gene, POD gene, chitinase gene, polyphenol oxidase (PPO) gene, and β -1, 3-glucanase (BG) gene, thus enhancing the resistance to *B. cinerea* [86]. SIARG2 contributed to MeJA-induced defense responses to *B. cinerea* in tomato fruit by regulating PRs, defensive enzyme activities, and arginine metabolism [85]. The mediator complex links transcription factors to the RNA polymerase II transcriptional machinery. Tomato mediator subunit 8 (SIMED8) is an essential component in JA-dependent defense response against B. cinerea [87]. JAZ proteins are repressors of the JA signaling pathway and have conserved Jas and ZIM/TIFY domains. SIVQ15 could interact with JAZ1 and

positively affect the defense against *B. cinerea* [54]. The Jas domain binds the COI1 receptor and MYC2 transcription factor, and the ZIM domain binds other JAZ proteins and NINJA proteins [88]. When plant endogenous JA increased, the COI1-JA-JAZ ternary complex formed and then induced the degradation of JAZ protein [89], and then higher JA content brings resistance to *B. cinerea* [81].

3.3.2. Salicylic Acid

SA generally plays a role mainly in the infection of biotrophic pathogens. There are generally two pathways for SA synthesis, including the phenylalanine ammonia lyase (PAL) pathway and isochorismate synthase (ICS) pathway [89–91]. The expressions of SA-biosynthetic genes EDS1 (Enhanced Disease Susceptibility 1), PAD4 (Phytoalexin Deficient 4), and SA marker gene PR1 were increased in tomato upon *B. cinerea* infection. However, the expression of JA-biosynthetic gene LoxC (lipoxygenase) as well as two JAdependent genes, PI I and PI II (proteinase inhibitors I and II), were decreased upon B. cinerea infection [44]. SA induced substantial transcriptional expression [92], including downstream NPR1, PR, and some WRKY genes. NPR1 plays an important role in salicylicacid-induced plant immunity and can activate downstream PR1, PR2, and PR5 [93]. The defense pathways regulated by SA and JA are mutually antagonistic. For instance, SA activates the NPR1 gene, which repressed the PI gene activated by JA in tomato [94], and thus, knockdown of tomato SINPR1 via modulation of ROS homeostasis and JA/ET signaling enhances resistance to *B. cinerea* [39,85]. Rose RcTGA1 interacted with NPR1 to regulate plant resistance to *B. cinerea* [30]. Strawberry FaSnRK1 α increased the resistance of fruit to B. cinerea via SA signaling pathway, regulated the expression of six strawberry PR genes, and interacted with FaWRKY33.2 [95].

3.3.3. Ethylene

ET is a simple gaseous hormone with biological activity. Plants can regulate their physiological processes through ethylene biosynthesis and signal transduction pathways. The two enzymes of ethylene synthesis are ACS and ACO; ACS catalyzes the formation of ACC from AdoMet, and ACO catalyzes the conversion of ACC to ethylene [96]. Ethylene receptors including ETR1, ERS1, ETR2, ERS2, and EIN4 were identified [38,97–99]. CTR1 is a negative regulator of ethylene signaling pathway [100], and CTR1 is inactive in the presence of ethylene and active in the absence of ethylene [101]. EIN2 is a key regulator of the ethylene signaling pathway and its loss of function results in a complete loss of ethylene response in plants. In the absence of ethylene in plants, CTR1 phosphorylates the C-terminal domain of EIN2, EIN3, EIL1, and EIL2. The box proteins EBF1 and EBF2 are rapidly degraded by the ubiquitinated proteasome pathway. CTR1 fails to phosphorylate EIN2 in the presence of ethylene [102–105]. EIN3 is a core factor in the interaction between ethylene and other hormones. Both JAZ and MYC can affect the ethylene response pathway by inhibiting EIN3 [106]. Ethylene has been reported to increase resistance to *B. cinerea* in tomato, but the exact mechanism of action is unknown [71,107,108]. ERF is also a plant-specific transcription factor that usually functions in the last step of the ethylene transduction pathway, but ERF has also been reported to function in the JA and SA pathways, such as tomato SIERF2 [109], SIERF3b, and SIERF5 [110], which play a role in methyl jasmonate-induced resistance to B. cinerea. Tomato ERF. A1, ERF. B4, ERF. C3, and ERF. A3 belongs to the B3 Group as well as ERF. C1, C3, C4, C6, D2, D7, ERF. A4, B12, B13, D6, F4, and H9 were necessary for tomato resistance to B. cinerea, but the specific mechanism remains to be clarified [111,112]. ERF. A1, Pti5 (also named ERF. G2), Pti6 (also named ERF. C6), and ERF. A4) were increased in tomato response to B. cinerea infection [113], and Pti4 plays a crucial role in the response to *B. cinerea* infection [114]. Grapevine VaERF16, which interacts with VaMYB306, was induced by B. cinerea infection and positively modulated plant resistance to *B. cinerea* [115].

3.3.4. Other Hormones

Cytokinin (CTK) plays a positive role in the resistance to *B. cinerea*, while abscisic acid has an opposite role [58]. The other hormones have also been reported in crops. When *Vitis vinifera* was infected with *B. cinerea*, genes associated with the 'ABA biosynthetic process', 'ABA catabolic process', and 'response to ABA' were highly induced [116]. AUX, CTK, GAs, ABA, ET, brassinosteroid, JA, and SA signal transduction in grape berries and kiwifruits have changed to counter the *B. cinerea* [14]. Co-silencing of ABA receptors SIRCAR9, SIRCAR11, SIRCAR12, and SIRCAR13 weakened the ethylene biosynthesis and signaling pathway that enhanced fruit firmness and altered the shelf-life and susceptibility to *B. cinerea* [117]. AcTPR2, which is associated with IAA signaling pathways, confers resistance to *B. cinerea* [118]. All of these examples shed light on the role of phytohormones and their interaction with each other [75].

3.4. Other Proteins

In addition to the reported major proteins, other proteins also play a role in the resistance of *B. cinerea*. Tomato SIDQD/SDH2 plays a key role in flavonoid biosynthesis and fruit resistance to *B. cinerea* [119]. Strawberry MANNOSE-BINDING LECTIN 1 (MBL1) is a member of the G-type lectin family and was involved in plant defense against *B. cinerea* [120]. Loss-of-function tomato phosphoinositide specific phospholipase C2 SIPLC2 lines showed increased resistance to *B. cinerea* [121,122]. SIIMP3 functions as a bifunctional enzyme involved in the biosynthesis of AsA and myoinositol and increases fruit resistance to *B. cinerea* [123]. FaPG1 has a key role in remodeling pectins during strawberry softening and regulating plant resistance to *B. cinerea* [124]. Tomato β -1, 3-GLUCANASE10 (SIBG10) regulates fruit resistance to *B. cinerea* by modulating callose deposition [125].

Proteins	roteins Crops Genetic Techniques		References
RcTGA1	Rose	VIGS	[30]
SIDQD/SDH2	Tomato	CRISPR/Cas9	[119]
SITD2	Tomato	RNAi	[80]
SIPLC2	Tomato	CRISPR/Cas9, VIGS	[121,122]
SIPSKR1	Tomato	CRISPR/Cas9	[35]
SIRIPK	Tomato	VIGS	[16]
SIRCAR9, SIRCAR11, SIRCAR12, SIRCAR13	Tomato	RNAi	[117]
SIVQ15	Tomato	CRISPR/Cas9	[54]
SIBBX20	Tomato	CRISPR/Cas9	[81]
AcTPR2	Kiwifruit	VIGS	[118]
FaSnRK1 <i>a</i>	Strawberry	VIGS	[95]
SIARG2	Tomato	VIGS	[85]
FaPG1	Strawberry	CRISPR/Cas9	[124]
SIBG10	Tomato	CRISPR/Cas9	[125]
SIMED8	Tomato	antisense	[87]
SIMKK2, SIMKK4	Tomato	VIGS	[42]
SIMPK3	Tomato	CRISPR/Cas9	[44]
StMKK1	Potato	RNAi	[46]
FaMAPK19	Strawberry	antisense	[48]
SIDRW1	Tomato	VIGS	[50]
SIWRKY31	Tomato	CRISPR/Cas9	[54]
FvWRKY50	Strawberry	RNAi	[53]
FaWRKY25	Strawberry	RNAi	[52]
FaWRKY11	Strawberry	RNAi	[51]
RcWRKY41	Rose	VIGS	[56]

Table 1. Proteins and genetic techniques involved in resistance to *B. cinerea* in different horticultural crops.

Proteins	Crops	Genetic Techniques	References
RcWRKY13	Rose	VIGS	[58]
RcMYB84,	Rose	VIGS	[61]
RcMYB123			[]
VaMYB306	Grape	RNAi	[115]
SIJIG	Tomato	CRISPR/Cas9	[66]
SIMYC2	Tomato	CRISPR/Cas9	[68]

Table 1. Cont.

4. Natural Products That Can Enhance the Resistance to *B. cinerea* in Horticultural Crops

Though genetic improvement by altering the expression of the defense genes is an effective method, it is also urgent to search for natural products that can improve the resistance to *B. cinerea*.

4.1. Microbial Elicitors

Elicitors can activate plant defenses based on their recognition as putative pathogenassociated molecular patterns (PAMPs) [126], causing reactive oxygen species (ROS) burst, calcium (Ca²⁺) influx, mitogen-activated protein kinase (MAPK) activation, and defenserelated gene expression [127,128]. Several studies have identified *B. cinerea* elicitors that could induce plant immune responses. B. cinerea elicitors can be classified into two categories, including saccharide elicitors and protein elicitors [129]. Extracellular proteins secreted by B. cinerea, such as BcNEP1 and BcNEP2 [130], Xyn11A [131], BcSpl1 [132], and BcGs1 [133], can induce plant defenses. In the case of endopolygalacturonases [134] and xylanases [135], the ability to activate plant defenses is based on their recognition as pathogen-associated molecular patterns (PAMPs) by the plant immune system [126], causing reactive oxygen species (ROS) burst, calcium (Ca²⁺) influx, mitogen-activated protein kinase (MAPK) activation, and defense-related gene expression [127,128]. Intracellular proteins include effector proteins, which induce the resistance responses inside the plant cell, such as Bccrh1 [136] and BcSSP2 [137]. Chitin, the well-known fungal PAMP, is a polysaccharide made of N-acetyl-D-glucosamine (GlcNAc) and is the second most abundant polysaccharide after cellulose [138], which can also lead to plant immune response [139]. Several microbial elicitors, including chitin, AsES, BcGs1, Oli-D1, and Oli-D2, were proven to enhance the resistance to *B. cinerea* in horticultural crops (Table 2).

4.2. Plant Natural Products

Natural products from plants or phytohormones and their derivates were proven to enhance the resistance to *B. cinerea* in horticultural crops (Table 2). Melatonin is used to treat strawberry [140] and tomato [141], which shows great resistance to *B. cinerea*. In addition, 1-methylcyclopropene (1-MCP) [113,142] and 2, 5-norbornadiene [113] are useful in the ET signaling pathway. Phenylalanine is one of the essential amino acids and it can be used to control gray mold disease [143]. Ferulic acid is a phenolic acid commonly found in the cell walls of grains, vegetables, and fruit and it has a positive effect on defense against *B. cinerea* [19]. Piperonylic acid is the inhibitor of the phenylpropanoid pathway, which induces broad-spectrum disease resistance in tomato [144]. Moreover, the defense response against necrotrophic fungi is greatly dependent on phytohormones and the crosstalk between them [75]. Thus, it reminds us that certain concentrations of phytohormones and their derivates can help to control *B. cinerea*. 6-benzylaminopurine [58,73], zeatin [58], abscisic acid [58], salicylic Acid [74], MeJA [72,145–147], Ile [148], brassinosteroid [146,149], ethylene [113], and 1-aminocyclopropane-1-carboxylic acid [150] were also used for enhancing the resistance to *B. cinerea* in rose, tomato, and strawberry.

Category	Compound	Crops Species	Tissue	Concentration	Stage	References
Hormone- related natural products from plants		Rose	Petal	100 µM	Postharvest	[58]
	8-benzylanimopurme	Tomato	Leaf	$100 \; \mu L L^{-1}$	Postharvest	[73]
	Zeatin	Rose	Petal	100 µM	Postharvest	[58]
		Tomato	Fruit	10 mM	Postharvest	[72]
	MeJA	Strawberry	Leaf and petal	10 µM	Postharvest	[145]
		Rose	Petal	0.2 mM	Postharvest	[146,147]
	T 1.	Rose	Petal	10 mM	Postharvest	[1/8]
	lie	Strawberry	Fruit			[140]
	Provident in the state in the	Strawberry	Fruit	10 µM	Postharvest	[149]
	brassinosteroid	Rose	Petal	1 μΜ	Postharvest	[146]
	Ethylene	Tomato	Fruit	$1 \mu L L^{-1}$	Postharvest	[113]
	1-aminocyclopropane- 1-carboxylic acid	Rose	Petal	50 μM, 100 μM, 200 μM, 400 μM	Postharvest	[150]
	1-methylcyclopropene	Rose	Petal	$1 \mu L L^{-1}$	Postharvest	[142]
	2, 5-norbornadiene	Tomato	Fruit	$5 \ \mu L \ L^{-1}$	Postharvest	[113]
Microbial elicitors	chitin	Tomato	Fruit	0.5%	Postharvest	[151]
	AsES	Strawberry	Leaf	60 nM	Preharvest	[152]
	BcGs1	Tomato	Leaf	250 nM	Postharvest	[137]
	Oli-D1, Oli-D2	Tomato	Leaf	1 μΜ	Postharvest	[153]
Other natural products from plants	Malatanin	Strawberry	Fruit	100 µM	Postharvest	[140]
	Welatohin	Tomato	Fruit	0.1 mM	Preharvest	[141]
	Phenylalanine	Chrysanthemum	Petal	6 mM	Postharvest	[143]
	Ferulic acid	Tomato	Fruit	100 µM	Postharvest	[19]
	Piperonylic acid	Tomato	Leaf	300 µM	Postharvest	[144]

Table 2. Natural products used to control gray mold in horticultural crops.

5. Conclusions and Prospects

This review summarizes recent advances in mechanisms underlying defense responses of horticultural crops to *B. cinerea*, including physiological responses, change of metabolites, crucial proteins in PTI signaling pathways, TFs, and hormone pathways, which provides significant insights into horticultural crops against *B. cinerea*. These findings suggest that transcriptional regulation and hormone transduction pathways undoubtedly play important roles in the defense responses of horticultural crops to *B. cinerea*. However, there are few reports on epigenetic modification, phase separation, and other new regulatory aspects for underlying defense responses of horticultural crops to *B. cinerea*. Therefore, future research should focus on these new regulatory aspects.

We proposed approaches to improve horticultural crops resistance to *B. cinerea* by modifying genes including TFs, MAPK proteins, and some other proteins in different processes [154]. These abundant gene resources can not only improve plants disease resistance but also plants development and fruit quality [124,125]. Elicitors from *B. cinerea* and some other microbes can induce the resistance of horticultural crops to *B. cinerea* by inducing obvious plant defense responses [133,152]. Additionally, certain concentrations of natural products can also be used to control gray mold disease on horticultural crops.

Author Contributions: Conceptualization, Y.C. and R.L.; writing—review and editing, R.L. and Y.C.; funding acquisition, Y.C. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by National Key Research and Development Program of China (2018YFD1000407), Project of Chongqing Science and Technology Commission (cstc2021jcyj-msxmX0160 and CSTB2022NSCQ-MSX0959), and Chongqing Talents: Exceptional Young Talents Project (cstc2021ycjh-bgzxm0042).

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare that they have no conflict of interest.

References

- 1. Xu, X.; Chen, Y.; Li, B.; Zhang, Z.; Qin, G.; Chen, T.; Tian, S. Molecular mechanisms underlying multi-level defense responses of horticultural crops to fungal pathogens. *Hortic. Res.* 2022, *9*, uhac066. [CrossRef] [PubMed]
- 2. Weiberg, A.; Wang, M.; Lin, F.-M.; Zhao, H.; Zhang, Z.; Kaloshian, I.; Huang, H.-D.; Jin, H. Fungal small RNAs suppress plant immunity by hijacking host RNA interference pathways. *Science* **2013**, *342*, 118–123. [CrossRef] [PubMed]
- Van Baarlen, P.; Woltering, E.J.; Staats, M.; Van Kan, J.A.L. Histochemical and genetic analysis of host and non-host interactions of Arabidopsis with three *Botrytis* species: An important role for cell death control. *Mol. Plant Pathol.* 2007, *8*, 41–54. [CrossRef] [PubMed]
- Williamson, B.; Tudzynski, B.; Tudzynski, P.; Van Kan, J.A.L. *Botrytis cinerea*: The cause of grey mould disease. *Mol. Plant Pathol.* 2007, *8*, 561–580. [CrossRef] [PubMed]
- 5. Ciliberti, N.; Fermaud, M.; Roudet, J.; Rossi, V. Environmental conditions affect *Botrytis cinerea* infection of mature grape berries more than the strain or transposon genotype. *Phytopathology* **2015**, *105*, 1090–1096. [CrossRef] [PubMed]
- 6. Elmer, P.A.G.; Michailides, T.J.; Elad, Y.; Williamson, B.; Tudzynski, P.; Delen, N. Epidemiology of *Botrytis cinerea* in orchard and vine crops. In *Botrytis: Biology, Pathology and Control*; Springer: Dordrecht, The Netherlands, 2007; pp. 243–272.
- 7. Mengiste, T. Plant immunity to necrotrophs. Annu. Rev. Phytopathol. 2012, 50, 267–294. [CrossRef] [PubMed]
- 8. Abu Qamar, S.F.; Moustafa, K.; Tran, L.-S.P. 'Omics' and plant responses to *Botrytis cinerea*. *Front. Plant Sci.* **2016**, *7*, 1658. [PubMed]
- 9. Petrasch, S.; Knapp, S.J.; van Kan, J.A.L.; Blanco-Ulate, B. Grey mould of strawberry, a devastating disease caused by the ubiquitous necrotrophic fungal pathogen *Botrytis cinerea*. *Mol Plant Pathol.* **2019**, *20*, 877–892. [CrossRef]
- 10. Liao, C.-J.; Hailemariam, S.; Sharon, A.; Mengiste, T. Pathogenic strategies and immune mechanisms to necrotrophs: Differences and similarities to biotrophs and hemibiotrophs. *Curr. Opin. Plant Biol.* **2022**, *69*, 102291. [CrossRef]
- AbuQamar, S.; Moustafa, K.; Tran, L.S. Mechanisms and strategies of plant defense against *Botrytis cinerea*. Crit. Rev. Biotechnol. 2017, 37, 262–274. [CrossRef]
- 12. Torres, M.A. ROS in biotic interactions. *Physiol. Plant.* 2010, 138, 414–429. [CrossRef]
- Bui, T.T.; Wright, S.A.; Falk, A.B.; Vanwalleghem, T.; Van Hemelrijck, W.; Hertog, M.L.; Keulemans, J.; Davey, M.W. *Botrytis cinerea* differentially induces postharvest antioxidant responses in 'Braeburn' and 'Golden Delicious' apple fruit. *J. Sci. Food Agric.* 2019, 99, 5662–5670. [CrossRef] [PubMed]
- 14. Song, Z.; Pang, Q.; Lu, S.; Yu, L.; Pervaiz, T.; Fu, W.; Jia, H.; Fang, J. Transcriptomic and metabolmic approaches to counter the effect of *Botrytis cinerea* in grape berry with the application of nitric oxide. *Sci. Hortic.* **2022**, 296, 110901. [CrossRef]
- Liu, M.; Zhang, Q.; Wang, C.; Meng, T.; Wang, L.; Chen, C.; Ren, Z. CsWRKY10 mediates defence responses to *Botrytis cinerea* infection in Cucumis sativus. *Plant Sci.* 2020, 300, 110640. [CrossRef] [PubMed]
- 16. Wang, R.; Li, C.; Li, Q.; Ai, Y.; Huang, Z.; Sun, X.; Zhou, J.; Zhou, Y.; Liang, Y. Tomato receptor-like cytosolic kinase RIPK confers broad-spectrum disease resistance without yield penalties. *Hortic. Res.* **2022**, *9*, uhac207. [CrossRef] [PubMed]
- 17. Gupta, K.J.; Fernie, A.R.; Kaiser, W.M.; van Dongen, J.T. On the origins of nitric oxide. *Trends Plant Sci.* 2011, 16, 160–168. [CrossRef]
- Li, R.; Sheng, J.; Shen, L. Nitric oxide plays an important role in β-aminobutyric acid-induced resistance to *Botrytis cinerea* in tomato plants. *Plant Pathol. J.* 2020, *36*, 121–132. [CrossRef] [PubMed]
- 19. Shu, P.; Li, Y.; Wang, X.; Yao, L.; Sheng, J.; Shen, L. Exogenous ferulic acid treatment increases resistance against *Botrytis cinerea* in tomato fruit by regulating nitric oxide signaling pathway. *Postharvest Biol. Technol.* **2021**, *182*, 111678. [CrossRef]
- Lacrampe, N.; Colombié, S.; Dumont, D.; Nicot, P.; Lecompte, F.; Lugan, R. Nitrogen-mediated metabolic patterns of susceptibility to *Botrytis cinerea* infection in tomato (*Solanum lycopersicum*) stems. *Planta* 2023, 257, 41. [CrossRef]
- Nawrocka, J.; Szymczak, K.; Maćkowiak, A.; Skwarek-Fadecka, M.; Małolepsza, U. Determination of reactive oxygen or nitrogen species and novel volatile organic compounds in the defense responses of tomato plants against *Botrytis cinerea* induced by *Trichoderma virens* TRS 106. *Cells* 2022, 11, 3051. [CrossRef]
- 22. Zheng, Y.; Shen, L.; Yu, M.; Fan, B.; Zhao, D.; Liu, L.; Sheng, J. Nitric oxide synthase as a postharvest response in pathogen resistance of tomato fruit. *Postharvest Biol. Technol.* **2011**, *60*, 38–46. [CrossRef]
- 23. Lai, T.; Wang, Y.; Li, B.; Qin, G.; Tian, S. Defense responses of tomato fruit to exogenous nitric oxide during postharvest storage. *Postharvest Biol. Technol.* 2011, 62, 127–132. [CrossRef]
- Małolepsza, U.; Różalska, S. Nitric oxide and hydrogen peroxide in tomato resistance: Nitric oxide modulates hydrogen peroxide level in o-hydroxyethylorutin-induced resistance to *Botrytis cinerea* in tomato. *Plant Physiol. Biochem.* 2005, 43, 623–635. [CrossRef] [PubMed]
- 25. Floryszak-Wieczorek, J.; Arasimowicz-Jelonek, M. Contrasting regulation of NO and ROS in potato defense-associated metabolism in response to pathogens of different lifestyles. *PLoS ONE* **2016**, *11*, e0163546. [CrossRef] [PubMed]
- Delledonne, M.; Murgia, I.; Ederle, D.; Sbicego, P.F.; Biondani, A.; Polverari, A.; Lamb, C. Reactive oxygen intermediates modulate nitric oxide signaling in the plant hypersensitive disease-resistance response. *Plant Physiol. Biochem.* 2002, 40, 605–610. [CrossRef]
- Delledonne, M.; Zeier, J.; Marocco, A.; Lamb, C. Signal interactions between nitric oxide and reactive oxygen intermediates in the plant hypersensitive disease resistance response. *Proc. Natl. Acad. Sci. USA* 2001, *98*, 13454–13459. [CrossRef] [PubMed]

- Blanco-Ulate, B.; Amrine, K.C.; Collins, T.S.; Rivero, R.M.; Vicente, A.R.; Morales-Cruz, A.; Doyle, C.L.; Ye, Z.; Allen, G.; Heymann, H.; et al. Developmental and metabolic plasticity of white-skinned grape berries in response to *Botrytis cinerea* during noble rot. *Plant Physiol.* 2015, 169, 2422–2443. [CrossRef] [PubMed]
- Camanes, G.; Scalschi, L.; Vicedo, B.; Gonzalez-Bosch, C.; Garcia-Agustin, P. An untargeted global metabolomic analysis reveals the biochemical changes underlying basal resistance and priming in *Solanum lycopersicum*, and identifies 1-methyltryptophan as a metabolite involved in plant responses to *Botrytis cinerea* and *Pseudomonas syringae*. *Plant J.* 2015, *84*, 125–139.
- 30. Gao, P.; Zhang, H.; Yan, H.; Wang, Q.; Yan, B.; Jian, H.; Tang, K.; Qiu, X. RcTGA1 and glucosinolate biosynthesis pathway involvement in the defence of rose against the necrotrophic fungus *Botrytis cinerea*. *BMC Plant Biol.* **2021**, *21*, 223. [CrossRef]
- 31. Hu, Z.; Chang, X.; Dai, T.; Li, L.; Liu, P.; Wang, G.; Liu, P.; Huang, Z.; Liu, X. Metabolic profiling to identify the latent infection of strawberry by *Botrytis cinerea*. *Evol. Bioinform*. **2019**, *15*, 1176934319838518. [CrossRef]
- Wang, S.; Pang, Y.; Tao, Y.; Shi, X.; Zhang, Y.; Wang, Y.; Jiang, Y.; Ji, X.; Wang, B.; Herrera-Balandrano, D.D.; et al. Dipicolinic acid enhances kiwifruit resistance to *Botrytis cinerea* by promoting phenolics accumulation. *Pest Manag. Sci.* 2023, 79, 3177–3189. [CrossRef] [PubMed]
- Zhang, L.; Yuan, L.; Staehelin, C.; Li, Y.; Ruan, J.; Liang, Z.; Xie, Z.; Wang, W.; Xie, J.; Huang, S. The LYSIN MOTIF-CONTAINING RECEPTOR-LIKE KINASE 1 protein of banana is required for perception of pathogenic and symbiotic signals. *New Phytol.* 2019, 223, 1530–1546. [CrossRef] [PubMed]
- 34. Ai, Y.; Li, Q.; Li, C.; Wang, R.; Sun, X.; Chen, S.; Cai, X.-Z.; Qi, X.; Liang, Y. Tomato LysM receptor kinase 4 mediates chitin-elicited fungal resistance in both leaves and fruit. *Hortic. Res.* **2023**, *10*, uhad082. [CrossRef] [PubMed]
- Hu, Z.; Fang, H.; Zhu, C.; Gu, S.; Ding, S.; Yu, J.; Shi, K. Ubiquitylation of PHYTOSULFOKINE RECEPTOR 1 modulates the defense response in tomato. *Plant Physiol.* 2023, 192, 2507–2522. [CrossRef] [PubMed]
- Liu, X.; Wang, Z.; Tian, Y.; Zhang, S.; Li, D.; Dong, W.; Zhang, C.; Zhang, Z. Characterization of wall-associated kinase/wall-associated kinase-like (WAK/WAKL) family in rose (*Rosa chinensis*) reveals the role of RcWAK4 in *Botrytis* resistance. *BMC Plant Biol.* 2021, 21, 526. [CrossRef] [PubMed]
- 37. Wang, Z.; Ma, Y.; Chen, M.; Da, L.; Su, Z.; Zhang, Z.; Liu, X. Comparative genomics analysis of WAK/WAKL family in Rosaceae identify candidate WAKs involved in the resistance to *Botrytis cinerea*. *BMC Genom*. **2023**, 24, 337. [CrossRef] [PubMed]
- Bleecker, A.B.; Estelle, M.A.; Somerville, C.; Kende, H. Insensitivity to ethylene conferred by a dominant mutation in *Arabidopsis* thaliana. Science 1988, 241, 1086–1089. [CrossRef] [PubMed]
- Li, R.; Li, Y.; Zhang, Y.; Sheng, J.; Zhu, H.; Shen, L. Transcriptome analysis reveals that SINPR1 mediates tomato fruit resistance against *Botrytis cinerea* by modulating phenylpropanoid metabolism and balancing ROS homeostasis. *Postharvest Biol. Technol.* 2020, 172, 111382. [CrossRef]
- Zhang, J.; Li, W.; Xiang, T.; Liu, Z.; Laluk, K.; Ding, X.; Zou, Y.; Gao, M.; Zhang, X.; Chen, S.; et al. Receptor-like cytoplasmic kinases integrate signaling from multiple plant immune receptors and are targeted by a *Pseudomonas syringae* effector. *Cell Host Microbe* 2010, 7, 290–301. [CrossRef]
- Wang, D.; Wei, L.; Liu, T.; Ma, J.; Huang, K.; Guo, H.; Huang, Y.; Zhang, L.; Zhao, J.; Tsuda, K.; et al. Suppression of ETI by PTI priming to balance plant growth and defense through an MPK3/MPK6-WRKYs-PP2Cs module. *Mol. Plant.* 2023, *16*, 903–918. [CrossRef]
- 42. Li, X.; Zhang, Y.; Huang, L.; Ouyang, Z.; Hong, Y.; Zhang, H.; Li, D.; Song, F. Tomato SIMKK2 and SIMKK4 contribute to disease resistance against *Botrytis cinerea*. *BMC Plant Biol*. **2014**, *14*, 166. [CrossRef] [PubMed]
- Zheng, Y.; Yang, Y.; Liu, C.; Chen, L.; Sheng, J.; Shen, L. Inhibition of SIMPK1, SIMPK2, and SIMPK3 disrupts defense signaling pathways and enhances tomato fruit susceptibility to *Botrytis cinerea*. J. Agric. Food Chem. 2015, 63, 5509–5517. [CrossRef] [PubMed]
- 44. Zhang, S.; Wang, L.; Zhao, R.; Yu, W.; Li, R.; Li, Y.; Sheng, J.; Shen, L. Knockout of *SlMAPK3* Reduced Disease Resistance to *Botrytis cinerea* in Tomato Plants. *J. Agric. Food Chem.* **2018**, *66*, 8949–8956. [CrossRef] [PubMed]
- Zheng, Y.; Hong, H.; Chen, L.; Li, J.; Sheng, J.; Shen, L. LeMAPK1, LeMAPK2, and LeMAPK3 are associated with nitric oxideinduced defense response against *Botrytis cinerea* in the *Lycopersicon esculentum* fruit. *J. Agric. Food Chem.* 2014, 62, 1390–1396. [CrossRef] [PubMed]
- 46. Chen, X.; Wang, W.; Cai, P.; Wang, Z.; Li, T.; Du, Y. The role of the MAP kinase-kinase protein StMKK1 in potato immunity to different pathogens. *Hortic. Res.* 2021, *8*, 1–9. [CrossRef] [PubMed]
- Zhang, Y.; Long, Y.; Liu, Y.; Yang, M.; Wang, L.; Liu, X.; Zhang, Y.; Chen, Q.; Li, M.; Lin, Y.; et al. MAPK5 and MAPK10 overexpression influences strawberry fruit ripening, antioxidant capacity and resistance to *Botrytis cinerea*. *Planta* 2021, 255, 1–11. [CrossRef]
- 48. Zhang, G.; Jia, S.; Yan, Z.; Wang, Y.; Zhao, F.; Sun, Y. A strawberry mitogen-activated protein kinase gene, FaMAPK19, is involved in disease resistance against *Botrytis cinerea*. *Sci. Hortic.* **2020**, *265*, 109259. [CrossRef]
- 49. Yang, J.H.; Lee, K.; Du, Q.; Yang, S.; Yuan, B.; Qi, L.; Wang, H. A membrane-associated NAC domain transcription factor XVP interacts with TDIF co-receptor and regulates vascular meristem activity. *New Phytol.* **2019**, 226, 59–74. [CrossRef]
- Liu, B.; Hong, Y.-B.; Zhang, Y.-F.; Li, X.-H.; Huang, L.; Zhang, H.-J.; Li, D.-Y.; Song, F.-M. Tomato WRKY transcriptional factor SIDRW1 is required for disease resistance against *Botrytis cinerea* and tolerance to oxidative stress. *Plant Sci.* 2014, 227, 145–156. [CrossRef]

- 51. Wang, Y.; Zhao, F.; Zhang, G.; Jia, S.; Yan, Z. FaWRKY11 transcription factor positively regulates resistance to *Botrytis cinerea* in strawberry fruit. *Sci. Hortic.* **2020**, *279*, 109893. [CrossRef]
- 52. Jia, S.; Wang, Y.; Zhang, G.; Yan, Z.; Cai, Q. Strawberry *FaWRKY25* transcription factor negatively regulated the resistance of strawberry fruits to *Botrytis cinerea*. *Genes* **2020**, *12*, 56. [CrossRef] [PubMed]
- Ma, C.; Xiong, J.; Liang, M.; Liu, X.; Lai, X.; Bai, Y.; Cheng, Z. Strawberry WRKY transcription factor WRKY50 is required for resistance to necrotrophic fungal pathogen *Botrytis cinerea*. *Agronomy* 2021, *11*, 2377. [CrossRef]
- Huang, H.; Zhao, W.; Li, C.; Qiao, H.; Song, S.; Yang, R.; Sun, L.; Ma, J.; Ma, X.; Wang, S. SIVQ15 interacts with jasmonate-ZIM domain proteins and SIWRKY31 to regulate defense response in tomato. *Plant Physiol.* 2022, 190, 828–842. [CrossRef] [PubMed]
- Shu, P.; Zhang, S.; Li, Y.; Wang, X.; Yao, L.; Sheng, J.; Shen, L. Over-expression of SIWRKY46 in tomato plants increases susceptibility to *Botrytis cinerea* by modulating ROS homeostasis and SA and JA signaling pathways. *Plant Physiol. Biochem.* 2021, 166, 1–9. [CrossRef] [PubMed]
- Liu, X.; Li, D.; Zhang, S.; Xu, Y.; Zhang, Z. Genome-wide characterization of the rose (*Rosa chinensis*) WRKY family and role of RcWRKY41 in gray mold resistance. *BMC Plant Biol.* 2019, 19, 522. [CrossRef] [PubMed]
- Fu, Y.; Li, J.; Wu, H.; Jiang, S.; Zhu, Y.; Liu, C.; Xu, W.; Li, Q.; Yang, L. Analyses of *Botrytis cinerea*-responsive LrWRKY genes from Lilium regale reveal distinct roles of two LrWRKY transcription factors in mediating responses to *B. cinerea*. *Plant Cell Rep.* 2022, 41, 995–1012. [CrossRef] [PubMed]
- 58. Liu, X.; Zhou, X.; Li, D.; Hong, B.; Gao, J.; Zhang, Z. Rose WRKY13 promotes disease protection to *Botrytis* by enhancing cytokinin content and reducing abscisic acid signaling. *Plant Physiol.* **2022**, *191*, 679–693. [CrossRef]
- 59. Dubos, C.; Stracke, R.; Grotewold, E.; Weisshaar, B.; Martin, C.; Lepiniec, L. MYB transcription factors in *Arabidopsis*. *Trends Plant Sci.* **2010**, *15*, 573–581. [CrossRef]
- 60. Millard, P.S.; Kragelund, B.B.; Burow, M. R2R3 MYB transcription factors–functions outside the DNA-Binding domain. *Trends Plant Sci.* **2019**, *24*, 934–946. [CrossRef]
- 61. Ren, H.; Bai, M.; Sun, J.; Liu, J.; Ren, M.; Dong, Y.; Wang, N.; Ning, G.; Wang, C. RcMYB84 and RcMYB123 mediate jasmonateinduced defense responses against *Botrytis cinerea* in rose (*Rosa chinensis*). *Plant J.* **2020**, *103*, 1839–1849. [CrossRef]
- 62. Liu, M.; Zhang, Z.; Xu, Z.; Wang, L.; Chen, C.; Ren, Z. Overexpression of SIMYB75 enhances resistance to *Botrytis cinerea* and prolongs fruit storage life in tomato. *Plant Cell Rep.* **2020**, *40*, 43–58. [CrossRef] [PubMed]
- 63. Yin, Z.; Liu, J.; Zhao, H.; Chu, X.; Liu, H.; Ding, X.; Lu, C.; Wang, X.; Zhao, X.; Li, Y.; et al. SIMYB1 regulates the accumulation of lycopene, fruit shape, and resistance to *Botrytis cinerea* in tomato. *Hortic. Res.* **2022**, *10*, uhac282. [CrossRef] [PubMed]
- 64. Qian, Y.C.; Zhang, T.Y.; Yu, Y.; Gou, L.P.; Yang, J.T.; Xu, J.; Pi, E.X. Regulatory mechanisms of bHLH transcription factors in plant adaptive responses to various abiotic stresses. *Front. Plant Sci.* **2021**, *12*, 677611. [CrossRef] [PubMed]
- Pires, N.; Dolan, L. Origin and diversification of basic-helix-loop-helix proteins in plants. *Mol. Biol. Evol.* 2010, 27, 862–874. [CrossRef] [PubMed]
- Cao, Y.; Liu, L.; Ma, K.; Wang, W.; Lv, H.; Gao, M.; Wang, X.; Zhang, X.; Ren, S.; Zhang, N.; et al. The jasmonate-induced bHLH gene *SIJIG* functions in terpene biosynthesis and resistance to insects and fungus. *J. Integr. Plant Biol.* 2022, 64, 1102–1115. [CrossRef] [PubMed]
- 67. Ullah, I.; Yuan, W.; Uzair, M.; Li, S.; Rehman, O.U.; Nanda, S.; Wu, H. Molecular characterization of bHLH transcription factor family in Rose (*Rosa chinensis* Jacq.) under *Botrytis cinerea* Infection. *Horticulturae* 2022, *8*, 989. [CrossRef]
- Shu, P.; Li, Z.; Min, D.; Zhang, X.; Ai, W.; Li, J.; Zhou, J.; Li, Z.; Li, F.; Li, X. CRISPR/Cas9-mediated SIMYC2 mutagenesis adverse to tomato plant growth and MeJA-induced fruit resistance to *Botrytis cinerea*. J. Agric. Food Chem. 2020, 68, 5529–5538. [CrossRef]
- Liu, B.; Ouyang, Z.; Zhang, Y.; Li, X.; Hong, Y.; Huang, L.; Liu, S.; Zhang, H.; Li, D.; Song, F. Tomato NAC transcription factor SISRN1 positively regulates defense response against biotic stress but negatively regulates abiotic stress response. *PLoS ONE* 2014, 9, e102067. [CrossRef]
- Le Hénanff, G.; Profizi, C.; Courteaux, B.; Rabenoelina, F.; Gérard, C.; Clément, C.; Baillieul, F.; Cordelier, S.; Dhondt-Cordelier, S. Grapevine NAC1 transcription factor as a convergent node in developmental processes, abiotic stresses, and necrotrophic/biotrophic pathogen tolerance. *J. Exp. Bot.* 2013, *64*, 4877–4893. [CrossRef]
- 71. Lu, C.K.; Liang, G. Fe deficiency-induced ethylene synthesis confers resistance to *Botrytis cinerea*. *New Phytol.* **2022**, 237, 1843–1855. [CrossRef]
- 72. Zhu, Z.; Tian, S. Resistant responses of tomato fruit treated with exogenous methyl jasmonate to *Botrytis cinerea* infection. *Sci. Hortic.* **2012**, *142*, 38–43. [CrossRef]
- 73. Gupta, R.; Pizarro, L.; Leibman-Markus, M.; Marash, I.; Bar, M. Cytokinin response induces immunity and fungal pathogen resistance, and modulates trafficking of the PRR LeEIX2 in tomato. *Mol. Plant Pathol.* **2020**, *21*, 1287–1306. [CrossRef] [PubMed]
- 74. Ha, S.T.T.; Kim, Y.-T.; Jeon, Y.H.; Choi, H.W.; In, B.-C. Regulation of *Botrytis cinerea* infection and gene expression in cut roses by using nano silver and salicylic acid. *Plants* **2021**, *10*, 1241. [CrossRef] [PubMed]
- 75. Denancé, N.; Sánchez-Vallet, A.; Goffner, D.; Molina, A. Disease resistance or growth: The role of plant hormones in balancing immune responses and fitness costs. *Front. Plant Sci.* **2013**, *4*, 155. [CrossRef] [PubMed]
- 76. Ishiguro, S.; Kawai-Oda, A.; Ueda, J.; Nishida, I.; Okada, K. The DEFECTIVE IN ANTHER DEHISCENCE1 gene encodes a novel phospholipase A1 catalyzing the initial step of jasmonic acid biosynthesis, which synchronizes pollen maturation, anther dehiscence, and flower opening in *Arabidopsis*. *Plant Cell*. 2001, 13, 2191–2209. [CrossRef] [PubMed]
- 77. Acosta, I.F.; Farmer, E.E. Jasmonates. Arab. Book 2010, 8, e0129. [CrossRef] [PubMed]

- Yu, M.; Shen, L.; Fan, B.; Zhao, D.; Zheng, Y.; Sheng, J. The effect of MeJA on ethylene biosynthesis and induced disease resistance to *Botrytis cinerea* in tomato. *Postharvest Biol. Technol.* 2009, 54, 153–158. [CrossRef]
- 79. Li, Z.; Wei, Y.; Cao, Z.; Jiang, S.; Chen, Y.; Shao, X. The jasmonic acid signaling pathway is associated with terpinen-4-ol-induced disease resistance against *Botrytis cinerea* in strawberry fruit. *J. Agric. Food Chem.* **2021**, *69*, 10678–10687. [CrossRef]
- Yeo, I.-C.; Manhaes, A.M.E.d.A.; Liu, J.; Avila, J.; He, P.; Devarenne, T.P. An unexpected role for tomato threonine deaminase 2 in host defense against bacterial infection. *Plant Physiol.* 2022, 192, 527–545. [CrossRef]
- Luo, D.; Sun, W.; Cai, J.; Hu, G.; Zhang, D.; Zhang, X.; Larkin, R.M.; Zhang, J.; Yang, C.; Ye, Z.; et al. SIBBX20 attenuates JA signalling and regulates resistance to *Botrytis cinerea* by inhibiting SIMED25 in tomato. *Plant Biotechnol. J.* 2023, 21, 792–805. [CrossRef]
- 82. Yan, J.; Zhang, C.; Gu, M.; Bai, Z.; Zhang, W.; Qi, T.; Cheng, Z.; Peng, W.; Luo, H.; Nan, F.; et al. The *Arabidopsis* coronatine insensitive1 protein is a jasmonate receptor. *Plant Cell* **2009**, *21*, 2220–2236. [CrossRef] [PubMed]
- Li, R.; Wang, L.; Li, Y.; Zhao, R.; Zhang, Y.; Sheng, J.; Ma, P.; Shen, L. Knockout of *SINPR1* enhances tomato plants resistance against *Botrytis cinerea* by modulating ROS homeostasis and JA/ET signaling pathways. *Physiol. Plant.* 2020, 170, 569–579. [CrossRef] [PubMed]
- 84. Tang, Q.; Zheng, X.-D.; Guo, J.; Yu, T. Tomato SlPti5 plays a regulative role in the plant immune response against *Botrytis cinerea* through modulation of ROS system and hormone pathways. *J. Integr. Agric.* **2022**, *21*, 697–709. [CrossRef]
- 85. Min, D.; Ai, W.; Zhou, J.; Li, J.; Zhang, X.; Li, Z.; Shi, Z.; Li, F.; Li, X.; Guo, Y. SIARG2 contributes to MeJA-induced defense responses to *Botrytis cinerea* in tomato fruit. *Pest Manag. Sci.* 2020, *76*, 3292–3301. [CrossRef] [PubMed]
- 86. Jia, H.; Zhang, C.; Pervaiz, T.; Zhao, P.; Liu, Z.; Wang, B.; Wang, C.; Zhang, L.; Fang, J.; Qian, J. Jasmonic acid involves in grape fruit ripening and resistant against *Botrytis cinerea*. *Funct. Integr. Genom.* **2016**, *16*, 79–94. [CrossRef] [PubMed]
- 87. Zhang, L.; Song, Y.; Liu, K.; Gong, F. The tomato mediator subunit MED8 positively regulates plant response to *Botrytis cinerea*. *J. Plant Physiol.* **2021**, *266*, 153533. [CrossRef] [PubMed]
- 88. Chung, H.S.; Howe, G.A. A critical role for the TIFY motif in repression of jasmonate signaling by a stabilized splice variant of the JASMONATE ZIM-domain protein JAZ10 in *Arabidopsis*. *Plant Cell*. **2009**, *21*, 131–145. [CrossRef] [PubMed]
- Zhang, G.; Yan, X.; Zhang, S.; Zhu, Y.; Zhang, X.; Qiao, H.; van Nocker, S.; Li, Z.; Wang, X. The jasmonate-ZIM domain gene VqJAZ4 from the Chinese wild grape *Vitis quinquangularis* improves resistance to powdery mildew in *Arabidopsis thaliana*. *Plant Physiol. Biochem.* 2019, 143, 329–339. [CrossRef]
- 90. Chen, Z.; Zheng, Z.; Huang, J.; Lai, Z.; Fan, B. Biosynthesis of salicylic acid in plants. *Plant Signal. Behav.* **2009**, *4*, 493–496. [CrossRef]
- 91. Métraux, J.-P. Recent breakthroughs in the study of salicylic acid biosynthesis. Trends Plant Sci. 2002, 7, 332–334. [CrossRef]
- 92. Ward, E.R.; Uknes, S.J.; Williams, S.C.; Dincher, S.S.; Wiederhold, D.L.; Alexander, D.C.; Ahl-Goy, P.; Metraux, J.-P.; Ryals, J.A. Coordinate gene activity in response to agents that induce systemic acquired resistance. *Plant Cell* 1991, *3*, 1085. [CrossRef] [PubMed]
- 93. Wang, K.; Li, C.; Lei, C.; Jiang, Y.; Qiu, L.; Zou, X.; Zheng, Y. β-aminobutyric acid induces priming defence against *Botrytis cinerea* in grapefruit by reducing intercellular redox status that modifies posttranslation of VvNPR1 and its interaction with VvTGA1. *Plant Physiol. Biochem.* 2020, 156, 552–565. [CrossRef] [PubMed]
- El Oirdi, M.; El Rahman, T.A.; Rigano, L.; El Hadrami, A.; Rodriguez, M.C.; Daayf, F.; Vojnov, A.; Bouarab, K. *Botrytis cinerea* manipulates the antagonistic effects between immune pathways to promote disease development in tomato. *Plant Cell.* 2011, 23, 2405–2421. [CrossRef] [PubMed]
- Luo, J.; Yu, W.; Xiao, Y.; Zhang, Y.; Peng, F. FaSnRK1α Mediates Salicylic Acid Pathways to Enhance Strawberry Resistance to Botrytis cinerea Manipulates the Antagonistic Effects between Immune Pathways to Promote Disease Development in Tomato. Hortic. Plant J. 2023; in press. [CrossRef]
- Chae, H.S.; Kieber, J.J. Eto Brute. Role of ACS turnover in regulating ethylene biosynthesis. *Trends Plant Sci.* 2005, 10, 291–296. [CrossRef] [PubMed]
- 97. Hua, J.; Chang, C.; Sun, Q.; Meyerowitz, E.M. Ethylene insensitivity conferred by *Arabidopsis* ERS gene. *Science* 1995, 269, 1712–1714. [CrossRef]
- 98. Hua, J.; Sakai, H.; Nourizadeh, S.; Chen, Q.G.; Bleecker, A.B.; Ecker, J.R.; Meyerowitz, E.M. EIN4 and ERS2 are members of the putative ethylene receptor gene family in *Arabidopsis*. *Plant Cell* **1998**, *10*, 1321–1332. [CrossRef] [PubMed]
- Chang, C.; Kwok, S.F.; Bleecker, A.B.; Meyerowitz, E.M. Arabidopsis ethylene-response gene ETR1: Similarity of product to two-component regulators. Science 1993, 262, 539–544. [CrossRef] [PubMed]
- 100. Kieber, J.J.; Rothenberg, M.; Roman, G.; Feldmann, K.A.; Ecker, J.R. CTR1, a negative regulator of the ethylene response pathway in arabidopsis, encodes a member of the Raf family of protein kinases. *Cell* **1993**, 72, 427–441. [CrossRef]
- Kendrick, M.D.; Chang, C. Ethylene signaling: New levels of complexity and regulation. *Curr. Opin. Plant Biol.* 2008, 11, 479–485.
 [CrossRef]
- 102. Ju, C.; Yoon, G.M.; Shemansky, J.M.; Lin, D.Y.; Ying, Z.I.; Chang, J.; Garrett, W.M.; Kessenbrock, M.; Groth, G.; Tucker, M.L.; et al. CTR1 phosphorylates the central regulator EIN2 to control ethylene hormone signaling from the ER membrane to the nucleus in Arabidopsis. *Proc. Natl. Acad. Sci. USA* 2012, 109, 19486–19491. [CrossRef]
- Guo, H.; Ecker, J.R. Plant responses to ethylene gas are mediated by SCFEBF1/EBF2-dependent proteolysis of EIN3 transcription factor. Cell 2003, 115, 667–677. [CrossRef] [PubMed]

- 104. Potuschak, T.; Lechner, E.; Parmentier, Y.; Yanagisawa, S.; Grava, S.; Koncz, C.; Genschik, P. EIN3-dependent regulation of plant ethylene hormone signaling by two *Arabidopsis* F box proteins: EBF1 and EBF2. *Cell* **2003**, *115*, 679–689. [CrossRef] [PubMed]
- 105. Binder, B.M.; Walker, J.M.; Gagne, J.M.; Emborg, T.J.; Hemmann, G.; Bleecker, A.B.; Vierstra, R.D. The Arabidopsis EIN3 binding F-box proteins EBF1 and EBF2 have distinct but overlapping roles in ethylene signaling. *Plant Cell* 2007, 19, 509–523. [CrossRef] [PubMed]
- 106. Ju, C.; Chang, C. Mechanistic Insights in ethylene perception and signal transduction. *Plant Physiol.* 2015, 169, 85–95. [CrossRef] [PubMed]
- 107. Diaz, J.; Have, A.T.; van Kan, J.A. The role of ethylene and wound signaling in resistance of tomato to *Botrytis cinerea*. *Plant Physiol*. **2002**, *129*, 1341–1351. [CrossRef] [PubMed]
- 108. Nambeesan, S.; Abu Qamar, S.; Laluk, K.; Mattoo, A.K.; Mickelbart, M.V.; Ferruzzi, M.G.; Mengiste, T.; Handa, A.K. Polyamines attenuate ethylene-mediated defense responses to abrogate resistance to *Botrytis cinerea* in tomato. *Plant Physiol.* 2011, 158, 1034–1045. [CrossRef] [PubMed]
- 109. Yu, W.; Zhao, R.; Sheng, J.; Shen, L. SIERF2 is associated with methyl jasmonate-mediated defense response against *Botrytis cinerea* in tomato fruit. *J. Agric. Food Chem.* **2018**, *66*, 9923–9932. [CrossRef]
- Alvarez-Gómez, T.B.; Ramírez-Trujillo, J.A.; Ramírez-Yáñez, M.; Suárez-Rodríguez, R. Overexpression of SIERF3b and SIERF5 in transgenic tomato alters fruit size, number of seeds and promotes early flowering, tolerance to abiotic stress and resistance to *Botrytis cinerea* infection. *Ann. Appl. Biol.* 2021, 179, 382–394. [CrossRef]
- 111. Ouyang, Z.; Liu, S.; Huang, L.; Hong, Y.; Li, X.; Huang, L.; Zhang, Y.; Zhang, H.; Li, D.; Song, F. Tomato SIERF.A1, SIERF.B4, SIERF.C3 and SIERF.A3, Members of B3 group of ERF family, are required for resistance to *Botrytis cinerea*. *Front. Plant Sci.* 2016, 7, 1964. [CrossRef]
- 112. Li, S.; Wu, P.; Yu, X.; Cao, J.; Chen, X.; Gao, L.; Chen, K.; Grierson, D. Contrasting roles of ethylene response factors in pathogen response and ripening in fleshy fruit. *Cells* **2022**, *11*, 2484. [CrossRef]
- 113. Zheng, H.; Jin, R.; Liu, Z.; Sun, C.; Shi, Y.; Grierson, D.; Zhu, C.; Li, S.; Ferguson, I.; Chen, K. Role of the tomato fruit ripening regulator MADS-RIN in resistance to *Botrytis cinerea* infection. *Food Qual. Saf.* **2021**, *5*, fyab028. [CrossRef]
- 114. Sun, Y.; Liang, B.; Wang, J.; Kai, W.; Chen, P.; Jiang, L.; Du, Y.; Leng, P. SlPti4 affects regulation of fruit ripening, seed germination and stress responses by modulating ABA signaling in tomato. *Plant Cell Physiol.* **2018**, *59*, 1956–1965. [CrossRef] [PubMed]
- 115. Zhu, Y.; Zhang, X.; Zhang, Q.; Chai, S.; Yin, W.; Gao, M.; Li, Z.; Wang, X. The transcription factors *VaERF16* and *VaMYB306* interact to enhance resistance of grapevine to *Botrytis cinerea* infection. *Mol. Plant Pathol.* **2022**, *23*, 1415–1432. [CrossRef] [PubMed]
- 116. Wan, R.; Guo, C.; Hou, X.; Zhu, Y.; Gao, M.; Hu, X.; Zhang, S.; Jiao, C.; Guo, R.; Li, Z.; et al. Comparative transcriptomic analysis highlights contrasting levels of resistance of *Vitis vinifera* and *Vitis amurensis* to *Botrytis cinerea*. *Hortic. Res.* 2021, *8*, 1–17. [CrossRef] [PubMed]
- 117. Zou, J.; Li, N.; Hu, N.; Tang, N.; Cao, H.; Liu, Y.; Chen, J.; Jian, W.; Gao, Y.; Yang, J.; et al. Co-silencing of ABA receptors (SIRCAR) reveals interactions between ABA and ethylene signaling during tomato fruit ripening. *Hortic. Res.* 2022, 9, uhac057. [CrossRef] [PubMed]
- 118. Li, Z.-X.; Lan, J.-B.; Liu, Y.-Q.; Qi, L.-W.; Tang, J.-M. Investigation of the role of AcTPR2 in kiwifruit and its response to *Botrytis cinerea* infection. *BMC Plant Biol.* 2020, 20, 557. [CrossRef] [PubMed]
- 119. Wang, R.; Liu, K.; Tang, B.; Su, D.; He, X.; Deng, H.; Wu, M.; Bouzayen, M.; Grierson, D.; Liu, M. The MADS-box protein SITAGL1 regulates a ripening-associated *SIDQD/SDH2* involved in flavonoid biosynthesis and resistance against *Botrytis cinerea* in post-harvest tomato fruit. *Plant J.* 2023, 115, 1746–1757. [CrossRef] [PubMed]
- Ma, L.; Haile, Z.M.; Sabbadini, S.; Mezzetti, B.; Negrini, F.; Baraldi, E. Functional characterization of MANNOSE-BINDING LECTIN 1, a G-type lectin gene family member, in response to fungal pathogens of strawberry. J. Exp. Bot. 2022, 74, 149–161. [CrossRef]
- 121. Perk, E.A.; Di Palma, A.A.; Colman, S.; Mariani, O.; Cerrudo, I.; D'ambrosio, J.M.; Robuschi, L.; Pombo, M.A.; Rosli, H.G.; Villareal, F.; et al. CRISPR/Cas9-mediated phospholipase C 2 knock-out tomato plants are more resistant to *Botrytis cinerea*. *Planta* 2023, 257, 1–6. [CrossRef]
- 122. Gonorazky, G.; Guzzo, M.C.; Abd-El-Haliem, A.M.; Joosten, M.H.; Laxalt, A.M. Silencing of the tomato phosphatidylinositolphospholipase C2 (SIPLC2) reduces plant susceptibility to *Botrytis cinerea*. *Mol. Plant Pathol.* **2016**, *17*, 1354–1363. [CrossRef]
- 123. Zheng, X.; Yuan, Y.; Huang, B.; Hu, X.; Tang, Y.; Xu, X.; Wu, M.; Gong, Z.; Luo, Y.; Gong, M.; et al. Control of fruit softening and Ascorbic acid accumulation by manipulation of *SlIMP3* in tomato. *Plant Biotechnol. J.* **2022**, *20*, 1213–1225. [CrossRef] [PubMed]
- 124. López-Casado, G.; Sánchez-Raya, C.; Ric-Varas, P.D.; Paniagua, C.; Blanco-Portales, R.; Muñoz-Blanco, J.; Pose, S.; Matas, A.J.; Mercado, J.A. CRISPR/Cas9 editing of the polygalacturonase FaPG1 gene improves strawberry fruit firmness. *Hortic. Res.* 2023, 10, uhad011. [CrossRef] [PubMed]
- 125. Pei, Y.; Xue, Q.; Zhang, Z.; Shu, P.; Deng, H.; Bouzayen, M.; Hong, Y.; Liu, M. β-1,3-GLUCANASE10 regulates tomato development and disease resistance by modulating callose deposition. *Plant Physiol.* **2023**, 192, 2785–2802. [CrossRef] [PubMed]
- González, M.; Brito, N.; González, C. The *Botrytis cinerea* elicitor protein BcIEB1 interacts with the tobacco PR5-family protein osmotin and protects the fungus against its antifungal activity. *New Phytol.* 2017, 215, 397–410. [CrossRef] [PubMed]
- 127. Yu, X.; Feng, B.; He, P.; Shan, L. From Chaos to Harmony: Responses and Signaling upon Microbial Pattern Recognition. *Annu. Rev. Phytopathol.* **2017**, *55*, 109–137. [CrossRef] [PubMed]

- 128. Yuan, M.; Jiang, Z.; Bi, G.; Nomura, K.; Liu, M.; Wang, Y.; Cai, B.; Zhou, J.-M.; He, S.Y.; Xin, X.-F. Pattern-recognition receptors are required for NLR-mediated plant immunity. *Nature* 2021, 592, 105–109. [CrossRef] [PubMed]
- 129. Guo, J.; Cheng, Y. Advances in fungal elicitor-triggered plant immunity. Int. J. Mol. Sci. 2022, 23, 12003. [CrossRef] [PubMed]
- Arenas, Y.C.; Kalkman, E.R.; Schouten, A.; Dieho, M.; Vredenbregt, P.; Uwumukiza, B.; Ruiz, M.O.; van Kan, J.A. Functional analysis and mode of action of phytotoxic Nep1-like proteins of *Botrytis cinerea*. *Physiol. Mol. Plant Pathol.* 2010, 74, 376–386. [CrossRef]
- 131. Frías, M.; González, M.; González, C.; Brito, N. A 25-residue peptide from *Botrytis cinerea* xylanase bcxyn11a elicits plant defensess. *Front. Plant Sci.* **2019**, *10*, 474. [CrossRef]
- 132. Frías, M.; González, C.; Brito, N. BcSpl1, a cerato-platanin family protein, contributes to *Botrytis cinerea* virulence and elicits the hypersensitive response in the host. *New Phytol.* **2011**, *192*, 483–495. [CrossRef]
- 133. Yang, C.; Liang, Y.; Qiu, D.; Zeng, H.; Yuan, J.; Yang, X. Lignin metabolism involves *Botrytis cinerea* BcGs1- induced defense response in tomato. *BMC Plant Biol.* **2018**, *18*, 103. [CrossRef] [PubMed]
- 134. Zhang, L.; Kars, I.; Essenstam, B.; Liebrand, T.W.H.; Wagemakers, L.; Elberse, J.; Tagkalaki, P.; Tjoitang, D.; van den Ackerveken, G.; van Kan, J.A.L. Fungal endopolygalacturonases are recognized as microbe-associated molecular patterns by the *Arabidopsis* receptor-like protein RESPONSIVENESS TO BOTRYTIS POLYGALACTURONASES1. *Plant Physiol.* 2014, 164, 352–364. [CrossRef] [PubMed]
- 135. Yang, Y.; Yang, X.; Dong, Y.; Qiu, D. The *Botrytis cinerea* xylanase BcXyl1 modulates plant immunity. *Front. Microbiol.* **2018**, *9*, 2535. [CrossRef] [PubMed]
- 136. Bi, K.; Scalschi, L.; Jaiswal, N.; Mengiste, T.; Fried, R.; Sanz, A.B.; Arroyo, J.; Zhu, W.; Masrati, G.; Sharon, A. The *Botrytis cinerea* Crh1 transglycosylase is a cytoplasmic effector triggering plant cell death and defense response. *Nat. Commun.* 2021, 12, 1–15. [CrossRef]
- 137. Zhu, W.; Yu, M.; Xu, R.; Bi, K.; Yu, S.; Xiong, C.; Liu, Z.; Sharon, A.; Jiang, D.; Wu, M.; et al. *Botrytis cinerea* BcSSP2 protein is a late infection phase, cytotoxic effector. *Environ. Microbiol.* 2022, 24, 3420–3435. [CrossRef] [PubMed]
- 138. Latgé, J.-P. The cell wall: A carbohydrate armour for the fungal cell. Mol. Microbiol. 2007, 66, 279–290. [CrossRef] [PubMed]
- Wan, J.; Zhang, S.; Stacey, G. Activation of a mitogen-activated protein kinase pathway in *Arabidopsis* by chitin. *Mol. Plant Pathol.* 2004, *5*, 125–135. [CrossRef]
- 140. Promyou, S.; Raruang, Y.; Chen, Z.-Y. Melatonin treatment of strawberry fruit during storage extends its post-harvest quality and reduces infection caused by *Botrytis cinerea*. *Foods* **2023**, *12*, 1445. [CrossRef]
- 141. Li, S.; Cheng, Y.; Yan, R.; Liu, Y.; Huan, C.; Zheng, X. Preharvest spray with melatonin improves postharvest disease resistance in cherry tomato fruit. *Postharvest Biol. Technol.* 2022, 193, 112055. [CrossRef]
- 142. Ha, S.T.T.; Kim, Y.-T.; Yeam, I.; Choi, H.W.; In, B.-C. Molecular dissection of rose and *Botrytis cinerea* pathosystems affected by ethylene. *Postharvest Biol. Technol.* 2022, 194, 112104. [CrossRef]
- 143. Kumar, V.; Hatan, E.; Bar, E.; Davidovich-Rikanati, R.; Doron-Faigenboim, A.; Spitzer-Rimon, B.; Elad, Y.; Alkan, N.; Lewinsohn, E.; Oren-Shamir, M. Phenylalanine increases chrysanthemum flower immunity against *Botrytis cinerea* attack. *Plant J.* 2020, 104, 226–240. [CrossRef] [PubMed]
- 144. Desmedt, W.; Jonckheere, W.; Nguyen, V.H.; Ameye, M.; De Zutter, N.; De Kock, K.; Debode, J.; Van Leeuwen, T.; Audenaert, K.; Vanholme, B.; et al. The phenylpropanoid pathway inhibitor piperonylic acid induces broad-spectrum pest and disease resistance in plants. *Plant Cell Environ.* 2021, 44, 3122–3139. [CrossRef] [PubMed]
- 145. Zhang, Z.; Lu, S.; Yu, W.; Ehsan, S.; Zhang, Y.; Jia, H.; Fang, J. Jasmonate increases terpene synthase expression, leading to strawberry resistance to *Botrytis cinerea* infection. *Plant Cell Rep.* **2022**, *41*, 1243–1260. [CrossRef] [PubMed]
- 146. Naeemi, M.H.; Jari, S.K.; Zarinnia, V.; Fatehi, F. Changes in physio-biochemical status of cut of rose (*Rosa hybrida* L. cv. Samurai) flowers under methyl Jasmonate, brassinosteroid, and fungal elicitor to control gray mold. *Sci. Hortic.* 2022, 306, 111402. [CrossRef]
- 147. Hasanzadeh-Naemi, M.; Jari, S.K.; Zarrinnia, V.; Fatehi, F. The effect of exogenous methyl jasmonate and brassinosteroid on physicochemical traits, vase life, and gray mold disease of cut rose (*Rosa hybrida* L.) flowers. *J. Saudi Soc. Agric. Sci.* **2021**, 20, 467–475. [CrossRef]
- 148. Li, Y.; Li, S.; Du, R.; Wang, J.; Li, H.; Xie, D.; Yan, J. Isoleucine enhances plant resistance against *Botrytis cinerea* via jasmonate signaling pathway. *Front. Plant Sci.* 2021, *12*, 628328. [CrossRef]
- 149. Li, C.; Wang, K.; Tan, M.; Lei, C.; Cao, S. Involvement of a receptor-like kinase complex of FvFLS2 and FvBAK1 in brassinosteroidsinduced immunity in postharvest strawberry fruit. *Postharvest Biol. Technol.* **2023**, *198*, 112266. [CrossRef]
- 150. Cao, X.; Yan, H.; Liu, X.; Li, D.; Sui, M.; Wu, J.; Yu, H.; Zhang, Z. A detached petal disc assay and virus-induced gene silencing facilitate the study of *Botrytis cinerea* resistance in rose flowers. *Hortic. Res.* **2019**, *6*, 1–11. [CrossRef]
- 151. Sun, C.; Fu, D.; Jin, L.; Chen, M.; Zheng, X.; Yu, T. Chitin isolated from yeast cell wall induces the resistance of tomato fruit to *Botrytis cinerea. Carbohydr. Polym.* **2018**, 199, 341–352. [CrossRef]
- 152. Perato, S.M.; Furio, R.N.; Tomas-Grau, R.H.; Caro, M.d.P.; Hael-Conrad, V.; Díaz-Ricci, J.C.; Martinez-Zamora, M.G. The fungal elicitor AsES requires a functional ethylene pathway to activate the innate immunity in strawberry. *Plant Biol.* **2020**, *22*, 1030–1040. [CrossRef]

- 153. Ouyang, Z.; Li, X.; Huang, L.; Hong, Y.; Zhang, Y.; Zhang, H.; Li, D.; Song, F. Elicitin-like proteins Oli-D1 and Oli-D2 from *Pythium oligandrum* trigger hypersensitive response in *Nicotiana benthamiana* and induce resistance against *Botrytis cinerea* in tomato. *Mol. Plant Pathol.* 2015, 16, 238–250. [CrossRef]
- 154. Bi, K.; Liang, Y.; Mengiste, T.; Sharon, A. Killing softly: A roadmap of *Botrytis cinerea* pathogenicity. *Trends Plant Sci.* 2022, 28, 211–222. [CrossRef]

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.