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Genetic Modification of Plant Hormones Induced by Parasitic Nematodes, Virus, Viroid, Bacteria, and Phytoplasma in Plant Growing

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Abstract

Plant hormones, such as auxin, play crucial roles in many plant developmental processes, which is crosstalk with gibberellin and strigolactone. The roles of hormones may vary in the biosynthesis of metabolisms. During the pathogen attack, including plant-parasitic nematodes, viroid, phytoplasma, virus, and bacteria, plant hormones are involved in several plant processes. Ethylene (ET), salicylate (SA), jasmonate (JA), and abscisic acid (ABA) primarily regulate synergistically or antagonistically against pathogens. Those pathogens—nematodes, bacteria, viroid, phytoplasma, and viruses regulate several plant hormones for successful parasitism, influencing the phytohormone structure and modifying plant development. Several genes are related to plant hormones that are involved in pathogens parasitism. In this chapter, how pathogens affect plant hormones in plants growing are discussed.

Keywords: plant hormones, gene, parasitic nematodes, bacteria, virus, phytoplasma, viroid, phytoplasma

1. Introduction

Plant hormones, small chemicals, also termed phytohormones, play an amazing array of very important roles in plant development, fruit ripening, from embryogenesis to senescence and stress resistance. Among the nine well-characterized plant hormones, gibberellin (GA), strigolactones (SLs), brassinosteroids (BRs), cytokinins (CKs), and auxin are classified as growth-promoting hormones, and others, including jasmonic acid (JA), salicylic acid (SA), ethylene, and abscisic acid (ABA) are considered stress reaction hormones. Several studies reveal that the role of hormones in the regulation of several physiological processes in diverse tissues or dissimilar ecological conditions has widely been described [1, 2]. Although little is known about the interaction between hormones at various levels of these cascades nevertheless, with the initiation of “omics” tools, noteworthy development has been made in the description of phytohormone reactions in different stimuli [3].

Although there are many studies in which exogenously hormone treatment is made to increase the plant quality [4], plant hormones are generated by the plants themselves, and their functions and chemical structures are mainly conserved among plants. Since these combinations are signal molecules, their cellular intensities are firmly controlled at the level of catabolism, biosynthesis, and transport in reaction to growing and ecological conditions. Therefore, here we have surveyed the published literature on the role of phytohormones in the perspective of their effects on numerous features of plant growth and respond to biotic stress conditions, such as plant-parasitic nematodes, virus, viroid, bacteria, and phytoplasma, and describe ways in which phytohormones modulate these reactions separately or grouping with several hormones. In addition to biotic stress and hormone interactions, special attention is also paid to the tomato, a well-studied plant, for the molecular genetic investigation of succulent plant growth and fruit ripening.

2. The role of phytohormones in plant development fruits ripening

The hormone auxin plays a key role in organ development as well as in distinct aspects of plant growth and development, such as cell elongation, division, and differentiation. Among auxin hormones, indole-3-acetic acid (IAA) is the most abundant occurring form in plants. Leaf primordia are known as the major sites for the synthesis of auxins, but roots contain much higher levels of auxins due to the polar transport of this hormone [5]. Construction of adventitious root (AR) is an important developmental process in cutting propagation for the horticultural industry. AR formation is divided into three developmental stages—induction, initiation, and lengthening [6, 7], and it has been stated that auxin (IAA) regulates the formation of AR at almost every developmental stage of these three stages. Although *Arabidopsis thaliana* have been well characterized in terms of mechanism of AR formation, there is no detailed study in other species involving tomato in which stem cuttings readily form ARs that which them an ideal system to study AR formation in detail. It was shown that AR is formed in tomato stem cuttings after the perception of a wounding stimulus [8]. The effect of auxin on the transcriptional regulation of target genes, through Auxin Response Factors (ARFs), has been shown to have the potential involvement of many ARFs in a/biotic stress responses [9]. For example, overexpression of an auxin-responsive gene, *TaSAUR75*, in *Arabidopsis* altered root length and survival rate and higher expression of some stress-sensitive genes, increasing drought and salt tolerance [10]. ARF genes also govern the initiation of fruit set by the involvement of *SlARF8*, *SlARF7*, and *SlARF9* on plant fruit development through the interactions between the auxin- and GA-signaling pathways [11, 12]. During tomato fruit ripening, auxin induces ethylene biosynthesis through upregulation of both *ACS* and *ACO* genes, and *Sl-SAUR69*, auxin-related gene, plays an important role in the initiation of “system 2” ripening, where the fruit experiences high sensitivity to ethylene [13]. Abscisic acid (ABA) is one of the most important hormones in the response mechanism against stress conditions and plays an important role in germination, root development, drought tolerance, and growth [14]. It is the best-known stress signaling molecule in plants, and it defends plants from a/biotic stresses. Apart from this, ABA controls almost the entire process of fruit ripening by regulating the ABA-ethylene pathways [15]. Conserved pyrabactin resistance/pyrabactin resistance-like/regulatory component of ABA receptors (PYR/PYL/RCAR) sense the ABA and trigger a series of signaling events. The hormone is normally known as plant growth inhibitor. However, the experiments showed that ABA promotes growth on roots and shoots. For instance, exogenous treatment of ABA to plant shoots encourage

primary root (PR) growth [16]. The main function of ABA in plants reported that it has a key role in stress adaptation involved in drought and salinity stress. It has been shown that ABA accumulation increases up to 40 times in plants exposed to drought stress. Drought and salinity stresses activate ABA biosynthetic genes through activating ABA response genes by binding ABA-responsive elements (ABREs) located in their promoter regions and increasing ABA levels in plants [17]. Mutant plants that are insensitive to ABA have also been identified as sugar insensitive, indicating a strong correlation between ABA and sugar signaling [18]. It was recently shown that increased ABA hormone content mediates the expression of drought and salt stress-induced *OsSWEET13* and *OsSWEET15* genes, resulting in increased sucrose content in phloem and altered sucrose transporting in leaf and root tissues [19].

ABA also plays a key role in plant immunity, but this involvement is more complex than its involvement in abiotic stress responses because the effect of ABA on the resistance of plants to fungi appears to depend on several factors, such as the rate of increase of the hormone, the type of pathogen, source of ABA (endogenous or exogenous), or application method. ABA-mediated response against biotic stresses is not fully understood. However, ABA also affects the expression of genes encoding proteins associated with the plant's response to a/biotic stresses and the spread of pathogens in the plant [20]. The functions of ABA in the pathogen defense mechanism may generally be related to SA, JA, and ET, whose signals are in more pathogen defense than ABA signaling [21]. In other words, endogenous ABA and JA form a synergy and exhibit a complex antagonistic relationship with SA during the development of the pathogen [22]. Based on the current studies, the research on ABA has become increasingly detailed, covering all aspects of plant development, fruit ripening, and a/biotic stress conditions, from properties and physiological indicators to the molecular and cellular levels, with greater emphasis on the study of various mechanisms.

Ethylene is the simplest and first molecule discovered as a hormone in plants [23]. Ethylene is synthesized by plants and influences various developmental processes, such as seed germination, fruit ripening, senescence, as well as responses to various a/biotic stresses. The ethylene signal transduction pathway has been broadly investigated in tomatoes because ethylene affects many characteristics related to plant vigor, fruit ripening, and postharvest physiology and storage. Numerous transcription factors have been identified that participate in the fruit ripening mechanism by regulating ethylene responses. The role of ethylene in the regulation of fruit ripening has been extensively reviewed [24]. Besides plant growth and development, recent studies have emphasized the role of ethylene in regulating plant responses to various stress conditions [25]. Ethylene is one of the important positive mediators for stress tolerance against salinity in many plants, such as the *Arabidopsis* model plant, maize, and tomato [26, 27]. Ethylene enhanced seed germination in saline conditions by reducing the expression of *MsACO* and *MsERF8* genes in alfalfa, showing that ethylene improves salt tolerance in alfalfa via *MsETR2* dependent manner [28]. In another recent study, the application of 1-MCP (an ethylene precursor) and AVG (an ethylene biosynthesis inhibitor), respectively, increased and decreased the cold resistance of apple seedlings. This study suggested that *MdERF1B*, an ethylene signaling activator, is a potential regulatory module that integrates the cold and ethylene signaling pathways in apples [29]. It is clear that ethylene plays a very important role in plant adaptation under abiotic stress. However, it would be more useful to determine the molecular cocktail of the antagonistic and synergistic role of ethylene with other signaling cues.

In addition to abiotic stress conditions, the role of ethylene in plants exposed to biotic stress has been investigated in different plant species and different diseases. Molecular studies in plants have shown in plants that many plant hormone-regulated

pathways related to resistance to biotic stresses are stimulated by the pathogen through the biosynthesis of effector proteins [30]. However, the role of ethylene in host-defense mechanisms against pathogens is complex and could be controversial due to the conflicting roles that ethylene can increase susceptibility or resistance depending on the host-pathogen interaction studied [31]. However, recent evidence demonstrates that the ethylene signaling pathway is involved in the plant defense response against biotrophic and necrotrophic pathogens. In apple, over-expression of the *MdERF11* gene in apple callus significantly enhances resistance to *B. dothidea* infection, whereas down-regulation of the gene in apple callus reduced the resistance [28]. In a similar study, over-expression of *AcERF2*, an ethylene-responsive factor, increased the resistance against both fungal pathogen *B. cinerea* and bacterial pathogen Pst DC 3000 in transgenic plants by regulating the expression of biotic stress-responsive genes positively [32]. These results indicate that ethylene not only regulates several aspects of plant growth and fruit ripening but also participates in defense mechanisms against biotic stress factors.

Gibberellins (GAs) are another important hormone that controls plant growth by regulating various physiological mechanisms [33]. Like many other plant hormones, GAs play key roles in stem and root elongation, flowering, leaf enlargement, fruit senescence, seed germination, and increased fruit size. Exogenously applied studies have shown that GAs affect various physiological activities, such as vegetative growth, flowering fruit set, leaf area expansion, internode elongation, and can also increase biomass production, fruit weight, and dryness of plant organs [34, 35]. Apart from the roles associated with the growth and development of the plant, GAs play a critical role in defense against environmental stresses. Treatment with GAs has been reported to increase the resistance to salinity stress. The foliar application of GA3 successfully elevated salinity tolerance of tomato and sweet pepper seedlings up to 25 mM NaCl and 50 mM NaCl, respectively showing the positive effect of GA3 in plants treated with salinity stress [36]. Exogenous GA increased the survival rate of wheat seedlings by regulating antioxidant defense mechanisms and the glyoxalase system under drought stress [37]. Moreover, treatment of tomato fruits with GA3 effectively reduced chilling injury (CI) index in mature green tomato fruit during long-term cold storage by reducing the expression of the DELLA protein, which is known as a crucial GA signaling component and growth repressor [38]. These findings provide a comprehensive insight into the mechanisms by which GA mediates fruit tolerance against abiotic stress conditions.

Although GA has received less attention in the elucidation of signaling components involved in defense responses to biotic stress conditions. However, recent evidence shows that GA signaling components play an important role in plant disease resistance and sensitivity. It has been shown that DELLA proteins, which function as repressors in GA signaling pathways, control plant immune responses [39]. It was reported that overexpression of four *MeDELLAs* identified in cassava increased the disease resistance against cassava bacterial blight. In contrast, virus-induced gene silencing (VIGS) of the genes reduced the resistance with lower transcript levels of defense-related genes [40]. In a recent study, exogenous GA3 treatment promoted the resistance of rice to brown planthopper (BPH) [41]. Accumulating evidence suggests that GA and signaling components play important roles in regulating defense responses against a variety of pathogens too.

3. Phytohormone stimulating by plant-parasitic nematodes

Nematodes are mostly microscopic organisms that are found in many places on the earth, from oceans to continents. They may be parasitic or free-living that

plant-parasitic nematodes cause damage to crops in the world. Plant-parasitic nematodes infect many plants, including crops, vegetables, and fruit trees [42], and they are the most damaging group of plant pathogens [43]. Root-knot nematodes (*Meloidogyne* ss) are one of the most damaging nematode genera in the world, and they are sedentary endoparasitic nematodes. Root-knot nematodes modify cell wall molecular architecture in their feeding site termed giant cells in successful parasitism [44, 45]. Plants also respond to nematode as a resistance gene such as SlWRKY3 roles a resistance against *Meloidogyne javanica* activating plant hormone [46]. Root-knot nematodes form a feeding tube where the glands insert the stylet to release nematode secretions to employ plant resistance and construct a feeding place [47]. Cell wall thickness change induced by nematodes [48]. Nematodes damage plants by affecting the phytohormone structure and altering plant growth. Plant hormones—auxin and cytokinin involve in a vital role in establishing established nematode feeding sites [49]. Auxin, cytokinin, and ethylene involve in gall formation after root-knot nematode infection in plant roots and activates the formation [50–53]. Auxin plays a significant role in cell division and growth of plant roots [53] that it also plays a role in gall development and gall expansion in roots of *A. thaliana* after *Meloidogyne incognita* infection [54].

Phytohormones: auxins, cytokinins, gibberellins, abscisic acid, and peptide hormones involved in plant defense. But, signaling pathways, but their function in plant defense is not well understood [55], and they involve in gene expression of plant defense and assembly of defense molecules such as pathogenicity-like proteins (PR) [56], phytoalexins [57] phenylpropanoids [58]. During the nematode infection, the concentrations of plant hormones [59]. Auxin, ethylene, cytokinin, gibberellic acid, abscisic acid, nitric oxide, jasmonic acid, brassinosteroids, salicylic acid, and strigolactones are plant hormones [60]. It appears that plant growth hormones, particularly cytokinin and auxin, are central to the formation of pathogen/pest-infected plant galls [61]. Root-knot nematodes and cyst nematodes modify auxin homeostasis thru several approaches [62]. Nematodes can alter several plant hormones for successful parasitism. Each hormone may coordinately stimulate potato tuberization formation or suppresses [63].

Gibberellins have functions such as controlling growth, metabolic activity, reactive oxygen species (ROS) in reaction during abiotic and biotic stresses [64, 65]. Gibberellin, glycosyltransferases, and auxins involve in biosynthesis and inactivation pathways in the nematode resistance response and their involvement in jasmonate signaling and biotic stress response in soybean-root-knot nematode interactions [66]. Several proteins are involved in hormone perception and signaling cytokinin, gibberellic acid, auxin, ethylene, and jasmonate recognition [60, 67].

Several genes are dissimilarly expressed in reaction to nematodes associated with plant hormones [60]. Several hormones are involved in nematode feeding site formation, such as ethylene biosynthesis in feeding cell formation by cyst nematodes, cytokinin, and ethylene-mediated regulatory networks in feeding cell development [60]. Auxin or IAA (indole-3-acetic acid) is involved in several developmental processes in plants. Auxin-mediated regulatory networks in nematode feeding cells, polar auxin transport (*pat*) plays a role in feeding cell formation and variation of local auxin intensities by endoparasitic nematodes [60].

Stress-related genes are notable genes involved in glycosyltransferases, peroxidases, auxin-sensitive proteins, and gibberellin-regulated genes during the Root-knot nematode in soybean infection. In the resistance reaction, auxins gibberellin signal transduction and glycosyltransferases, revealing the key role of components of biosynthesis and deactivation pathways and their involvement in jasmonate signaling and redox homeostasis involve in responses to biotic stress [66].

Cytokinin signaling is activated at nematode feeding sites to respond against sugar beet cyst nematode infection in the Arabidopsis plant [68].

Plant-parasitic nematodes may regulate phytohormone pathways that auxin and cytokinin involve in the formation of root-knot nematode and cyst nematodes feeding site, and plant genes are involved in hormone pathways [69]. Jasmonic acid defense molecules and salicylic acid-related defense are involved in nematode-plant interactions [69]. Ethylene plays a role in plant susceptibility to root-knot nematode and cyst nematodes [69]. Arabidopsis REPRESSOR OF CYTOKININ DEFICIENCY 1 transports UDP-N-acetylglucosamine/UDP-N-acetylgalactosamine and regulates endoplasmic reticulum protein quality control and cytokinin [70]. A transcription factor, WRKY23, is regulated by auxins and prompted by the cyst nematode *Heterodera schachtii* [71].

4. Viroid-induced plant hormone alterations

Viroids are agents that can cause disease by infecting many agriculturally important crop groups (such as potatoes, tomatoes, hops, coconuts, and citrus fruits) and ornamental plants [72–74]. Although viroids cause symptoms similar to viral infections in plants, they have exceptional structural, functional, and evolutionary features. Viroids are RNA with a minute genome varying between 250 and 401 bases, single-stranded, circular, non-protein-coding, and autonomously replicating RNA [75, 76]. They need a host cell to reproduce. Viroids are the smallest highly structured infectious agents that do not have detectable mRNA activity and can reproduce spontaneously in susceptible plant species [77]. Unlike viruses, viroids that do not have protein-coding ability need RNA-dependent RNA polymerases in the host plant to perform the initiation and elongation of viral RNA strands in replication and use cellular pathways for the transport of proliferating viroids [78, 79]. To date, 33 viroid species belonging to eight genera and two families (Avsunviroidae and Pospiviroidae), accepted by the International Committee on Virus Taxonomy (ICTV), have been reported and recorded. Species belonging to these families have important changes in terms of replication mechanisms and where they reproduce in the cell [80, 81]. In viroid infection, symptoms may present as asymptomatic, mildly symptomatic, or severe symptomatic, according to the plant species and the variant of the agent and/or the early infection of the plant. The symptom severity observed in plants varies depending on abiotic factors, such as high temperature and light intensity, that affect viroid replication [72, 82, 83].

Potato spindle tuber viroid (PSTVd) is the first agent defined as viroid in potato (*Solanum tuberosum* L.) viroids [84]. It has been reported to cause intense symptoms in this plant, where it is the main host, and cause serious damage in large production areas [85]. PSTVd is asymptomatic in most plants but has a broad host range (*Solanaceae*, *Asteraceae*, *Gesneriaceae*, and *Lauraceae*). Among the most important symptomatic hosts are tomato (*Solanum lycopersicum* L.) [85] and pepper (*Capsicum annuum* L.) [86] plants. Until today, it is known that the resistance to viroids in cultivated plants is limited, and there are no naturally resistant plants. Viroid infection usually results in changes in the cellular functions of the host plant, including defense mechanism, signal transduction, hormone balance, and energy production [77]. Viroids' virulence mechanism is mediated either straightforwardly by their own genome or by single- or double-stranded RNAs (ss/dsRNAs) composed of its genome, and the symptoms that arise systemic infection are caused by small RNAs (sRNA) produced from the viroid, which is unknown to date. It can be a result of accumulation with plant features, either in the organelle where the viroid proliferates or in the cytoplasm thru its effort within the cell [72]. Application of

microarray analysis-based studies in viroid-pathogenicity study due to the low proliferation rate of viroids in the model plant *A. thaliana* [87–89]. It was determined that PSTVd infection caused an important modification in gene expression in one of four different genes in Rutgers tomato cultivar, similar to the result observed in CaLCuV infection in *A. thaliana* [90].

To date, things have been done about gene-specific events different from host diseases [91]. It is a mediator of plant hormones to signals in plant defense against plant organisms and in response to biological stress [92, 93]. Plant hormones as a whole took part in the regulation of defense; Hormones involved in plant defense, such as salicylic acid (SA), ethylene (ET), and jasmonic acid (JA), are significant in systemic gain in the fight against pathogens [94]. Brassinosteroid (BR-induced systemic defense against biotrophs, appearance as a system from the entity that differs in appearance from the SA mediated SAR and JA/ET from the entity that is different from the mediated disease [95, 96]. Plant hormones such as abscisic acid, auxins, cytokines, plant systems, and plant hormones such as gibberellins are those that have emerged as end-model choices because they alter plant system functioning and morphological responses [97]. Having simple structures and low systems, plant hormones, cell type, plant preference, and as well as organogenesis and apoptosis preference, is in the eye and Estel (Santner). They also play a role in defense against viruses [98]. Viroids, those with non-RNA-coding genomes, also stimulate defensive responses in plants for symptomatic. In its design as a model system, the expression of PSTVd factor and its hosts encoding products involved in viroid defense/stress response, growth propensity, preferred defense/stress response, development, and other functions has been overlooked [98].

In recent years, with the increase in microarray analyzes and transcriptome studies, data on the effect of different signaling pathways in viroid infection have been obtained [99]. SA is identified for its significant function in the plant defense reaction to diverse biotic and abiotic stresses [100, 101]. In many plant species, fungal, bacterial, or viral infection causes local and, to a reduced amount, systemic amassing of endogenous SA [102]. Viral contaminations may activate boosted SA quantities both in infected subordinate leaves that acquire a hypersensitive response (HR) and in uninfected higher leaves that improve systemic acquired resistance (SAR) [103, 104]. Many plant species such as tomatoes, soybeans, and potatoes can have basal SA levels significantly greater than the presence in tobacco and *A. thaliana* [105]. Application of SA to sensitive tobacco and other plant species infected with tobacco mosaic virus (TMV), Cucumber mosaic virus (CMV), and Potato X virus (PVX) increased resistance to these agents [106]. In addition, SA application in tobacco and potato-PVY interactions decreased viral increase and postponed the onset of disease symptoms [107].

To determine the plant-viroid interactions, it was revealed that there was rising in the expression of the NPR1 gene in the susceptible Rutgers tomato variety 21–30 days after the infection of the tomato with PSTVd (potato spindle tuber viroid). It was confirmed that the expression of both NPR1 and PR1 genes was increased in the PSTVd-infested plant [108]. In the transcriptome investigation of tomato plants infested with PSTVd, it was determined that there were noteworthy modifications in the expression of 93 genes linked to SA biogenesis and 146 genes associated with SA signaling [109]. In this way, it has provided a unique insight into the mechanisms underlying transcript profiling, gene resistance and basal defense mechanism for gene, biotrophy versus necrotrophy, and pathogenicity of vascular and non-vascular pathogens. In this way, genomic technologies have facilitated the systems-wide approach to incorporate distinctive structures in the interfaces of hosts and pathogens [110]. It has been determined that increased SA accumulation and external SA application in *Gynura aurantiaca* plants infested with Citrus exocortis viroid (CEVd)

[111] have a beneficial effect on alleviating the symptoms caused by CEVd [112]. In addition, PR1, PR2, and PR3 gene expression levels were increased in the leaves of the hop plant infested by Citrus bark cracking viroid (CBCVd) and/or Hop latent viroid (HLVd) [113]. In HSVd infected hop plants [114], It is suggested that the regulation of genes encoding SA-bound PR1 and PR4 proteins was not triggered. No important alterations in endogenous SA content are detected in the PSTVd-infested potato cultivars *Solanum laxum* and Désirée [115, 116]. The poor reaction of potato to SA in PSTVd contamination suggests that several still unrevealed salicylates play in signal transduction in potatoes. Gentisic acid (GA), a metabolic derived of SA, observes to accumulate in large amounts, even higher than SA, in tomato and *G. aurantiaca* plants infested with CEVd [117]. It has also been suggested that GA treatments can delay the onset of symptoms and that GA plays as a pathogen-derived signal in addition to SA for the stimulation of plant defense genes in tomatoes [118].

JA plays a significant role in plant growing and growth events such as reproduction, flower and fruit growth, root development, senescence [119], and jasmonates in injury [120], insect damage, and defense against pathogens were determined to be key signals in stress responses [121]. Although JA does not inhibit the systemic increase of viruses, it has been observed that external applications of JA can reduce viral replication [122]. Generally, it has been observed that JA and ET signaling pathways do synergistically in the plant defense mechanism [123], and both JA and SA are necessary for pathogen-associated molecular model (PAMP)-stimulated resistance reactions to potato [123]. While JA supports plant defense in the initial stages of viral contamination, it reduces plant resistance if applied in later stages [124]. In *Nicotiana benthamiana*, both SA and JA were required for systemic resistance to TMV, and inhibiting JA development significantly reduced subsequent SA accumulation, suggesting that the reverse had no effect, proposing that JA was required to motivate SA [125]. Evidence that JA-mediated signaling is involved in plant-viroid interactions in tomato plants infested with PSTVd is provided by genome-wide analyzes [108].

A transcriptome study in hops showed that the synthesis of JA biosynthesis and JA signaling pathways was triggered in HSVd-infected plant leaves [114]. While the expression of the LOX gene was decreased in complete tissues of the hop plant (leaf, flower, and cone) infected with asymptomatic HLVd and severe symptomatic CBCVd in the hops plant, the JAR1 gene revealed small fluctuations in gene expression compared to the plants without viroids, regardless of disease status. Decreases in the expression of the LOX gene in leaf samples of together plant groups indicate that this gene does not contribute significantly to the dwarfing of hops plants infected with CBCVd [113].

In a study on gene expression in the tomato-PSTVd interaction, JAZ and MYC2 genes were identified for JA signaling [109], while MYC2 is the main regulator of the JA signaling pathway, which triggers the transcription of initial JA-receptive genes, whereas, in jasmonate-induced transcription, it is found to have a dual role. Although there are different variants of PSTVd used in studies, systemic infection of Rutgers tomato cultivar with PSTVd was confirmed by increased accumulation of JA in plant leaves [126]. Significant amassing of endogenic JA and its precursor cis-OPDA was detected in plants of PSTVd-infected Désirée potato cultivar and *S. laxum* plants [115, 116]. However, no notable modifications in JA and cis-OPDA contented or appearance of related genes were observed in the tubers of infected potato plants, recommending the presence of organ-specific alterations in plant hormone reactions upon potato-PSTVd contamination. Deficiency of JA biosynthesis and signaling can cause male sterility [127] and undersized development of aerial plant parts, particularly in situations where endogenic gibberellins are reduced [128].

Brassinosteroids (BRs) are steroid phytohormones that have been widely studied for their early isolation and characterization [129]. Plant growth and development [130].

They also act in plant resistance by stimulating plant defense against viruses [95]. BRs have active roles in defensive plants in contradiction of several biotic and abiotic stresses [131, 132]. It has been determined that the application of brassinolide (BL) against TMV in tobacco reduces the lesions amount on tobacco leaves and increases resistance to TMV [95]. BL application also reduced symptom development in CMV-infected *Arabidopsis* [133]. The interaction of BR with other plant hormones is partly related to the ability of BR to confer stress tolerance through synergistic or antagonistic interfaces with additional stress plant hormones such as auxins, JA, gibberellins, SA, and ABA, [134].

When a different PSTVd variant was used on the same tomato cultivars, it caused a rise in the expression of some genes like brassinosteroid-6-oxidase 1, while decreased expression of the CPD gene was observed [108]. It was determined that PSTVd infection did not have a noteworthy influence on endogenous CS in infested tomato plants [126]. The function of BR-mediated signaling in plant reactions to viroid interfaces is highly dependent on the host-viroid grouping, and though BRs have a significant part in the regulation of plant immunity, it is not possible to predict the outcome due to the different mechanisms of action of BRs in plant-viroid infection.

The significance of plant hormones in the instruction of plant immunity is clear [135]. There is insufficient information to form a general model of the interaction of plant hormones during plant-viroid infections. Therefore, new research can help improve the product by adding phytohormones aimed at improving plant resistance/tolerance to viroids in the production program at the aquaculture stage.

5. The interaction of phytoplasma with plant hormones

Many yellow-type diseases were supposed to be caused by viruses until a group of Japanese researchers in 1967 saw microorganisms similar to animal mycoplasma through electron microscopy in the phloem of diseased plants. Later, these types of bacteria without a cell wall were called mycoplasma-like organisms (MLOs). [136]. In subsequent years, MLOs were named "*Candidatus phytoplasma*" with DNA-specific amplification and sequencing methods [137]. Phytoplasma 16S rRNA genes with sufficient diversity are greatly preserved and are used in classifications of phytoplasmas [137–140].

Despite having one of the smallest genomes among living organisms, phytoplasmas encode compound metabolic functions that enable them to network with their plant hosts [141, 142]. Phytoplasmas are of different sizes and shapes, they live and reproduce in environments with equal osmotic pressure provided by plant phloem and insect fluids, and it is still not possible to reproduce *in vitro* conditions. Phytoplasmas are plant diseases that spread violently and rapidly and can increase metabolic activities, such as plant shoot production, flower shape, and color change in their hosts. They also cause severe decline and death in infected plants. [143, 144]. Plants infected with phytoplasmas often show symptoms indicating that their growth regulators are severely affected. The characteristic symptoms are vigor and phyllodes of flowers, sterility, loss of apical dominance leading to witches' broom formation and proliferation of axillary buds, abnormal internode elongation, and general stunting [145, 146].

Phytoplasmas are transmitted by families of *Cicadellidae*, *Cixidae*, *Psyllidae*, *Delphacidae*, and *Derbidae* [147]. It has been determined that phytoplasmas are transmitted with transovarial and seeds in some insect and plant hosts [148–157]. Phytoplasmas are also efficiently spread by vegetative propagation like micropropagation parts, grafting, and cuttings [158–160].

Phytoplasma diseases were previously thought to affect the growth regulators of plant hosts. It is now recognized that the pathogenicity of phytoplasmas includes

certain effector proteins that have diverse effects on growth and other aspects of plant life. Phytoplasma effector proteins activate physiological events in cells that control symptom development in the plant. Such physiological changes in plants result from the effect of phytoplasma on hormonal, nutritional, developmental processes, and stress and the interaction of these changes with each other [161].

Plant hormones are small molecules that have important regulatory roles in plant growth, survival, and immunity [162–172]. Plant hormones also trigger plant defense mechanisms against pathogen attacks [173, 174]. Salicylic acid (SA), jasmonic acid (JA), and ethylene are known to be involved in plant immune reactions. Although there are not many studies on other plant hormones such as cytokinins, abscisic acid, auxins, brassinosteroids, gibberellic acid, and peptide hormones, it is known that these hormones also take place in plant defense systems. These hormones are important for plant defense mechanisms in pathogen attack, and the cooperation between hormones is preserved in plant species. Activation and regulation of hormones against pathogen attack depend on plant host-phytoplasma interaction [173–176].

SA is the plant hormone used against pathogens in plant defense and enables the Pathogenesis Related Protein (PR) protein genes to be activated. The PR-1, PR-2, and PR-5 proteins are used as molecular markers for monitoring SA-dependent gene expression [176–179]. Genes expressed in the presence of SA are up-regulated in phytoplasma-infected plants. In a study, PR proteins were up-regulated in phytoplasma-infected seedlings of garland chrysanthemum and Mexican lime infected with “*Ca. P. aurantifolia*.” When the mulberry phloem sap was infected with phytoplasma, the expression of PR-1 protein was increased [180–182]. SA-hormones activities are increased in the grapevine infected with the phytoplasma “*Ca. P. solani*” and flavescence dorée phytoplasma [183–187].

JA is an important plant hormone involved in the development processes in which stress reactions such as insect attack, injury, and drought are triggered [188, 189]. Significant variation in gene expression by JA signaling has been reported in the phytoplasma infected tobacco (infected with the “*Ca. Perrisia mali*”), grapevine (infected with bois noir; up-regulated PR-6 gene), tomato (infected with “*Ca. P. solani*” strain C; up-regulation of the PR-6 gene PIN2), coconut (infected with yellow decline phytoplasma; up-regulation of the PR-3 and PR- 10) [186, 190].

Ethylene is a minor gas hormone that regulates the expansion of organs such as leaves, flowers, and fruits in plants and is considered to have an effect on activating the plant defense system against pathogens [173, 191]. Ethylene signaling is generally in synergy with JA signaling and provides increased resistance to pathogen attack by the expression of certain defense genes [173]. Differentiation of gene expression by ethylene signaling has been reported in the phytoplasma infected Mexican lime (infected with “*Ca. P. aurantifolia*”), grapevine (infected with “*Ca. P. solani*” and “*Ca. P. asteris*”), *Paulownia fortunei* (paulownia witches’ broom phytoplasma) [183, 190, 192–195].

There are some researches that have revealed the plant-pathogen interactions of Indole-3-acetic acid (IAA) or auxin signaling in disease development [171, 196]. In one study, it was revealed that there was a significant differentiation in the level of IAA in phytoplasma-infected Mexican lime [197].

Cytokinins are an important group of plant hormones that involve in plant growth and development [161]. In a study, it is thought that the elevation of cytokinin in the flowers of *Catharanthus roseus* plants is caused by phytoplasma infection [198].

Genetic studies in recent years have been promising in understanding the disease capabilities of phytoplasmas, the plant-phytoplasma interaction, and the control of phytoplasma diseases in plants. These studies have also revealed the hormonal responses of plants to phytoplasma diseases and the resistance mechanisms they

have developed in the fight against the disease. However, it is obvious that there are still many unknowns waiting to be clarified in terms of the biological structure of phytoplasmas and the hormonal interactions of phytoplasma infected plants. When phytoplasma diseases and plant resistance mechanisms are understood, agricultural production with disease control will be possible over the next half-century.

6. Phytohormone-producing plant growth-promoting rhizobacteria

Plants have a greatly complicated defense system akin to the animal immune system. Unknown molecules or signals are recognized by plants from their own injured cells and their immune responses by triggering against the invader [199, 200]. Plant hormones play a part in the regulation of plant growth. They have important functions in the setting of immune reactions against pathogens, insects, and beneficial microorganisms. Signaling pathways are interrelated with a complex network. Plants have a huge organizing potential to adapt to the biotic environment rapidly. They employ inadequate resources for growing and trigger their immune system against attack by insects or pathogens.

Plant pests possess several mechanisms to operate the plant's hormone signaling interaction to overcome host immunity. Beneficial root-colonizing microorganisms can organize the hormone-regulated immune signaling system to keep a continued mutualistic life cycle [201].

Efficacious pathogens and insects may vigorously attack the plant immune system to launch a continued relationship. On the other hand, beneficial associations between plants and microbes are rarely found in nature. Beneficial microorganisms that are found in the roots or the rhizosphere considerably progress in plant growth. Because beneficial microorganisms are primarily recognized by plants as possible attackers, thus plant immune system is become activated; they also support the plant to withstand biotic or abiotic stress [202].

Beneficial plant-microbe associations are highly organized with coordination of plant immune responses that are significant for plant development and survival. The best-studied mutualistic microorganisms are mycorrhiza fungi, plant-growth-promoting rhizobacteria, fungi, and *Rhizobium* bacteria [203, 204].

Rhizobium bacteria fix atmospheric nitrogen for the plant by inducing the development of symbiotic constructions (nodules) in the roots of legumes [201].

Beneficial PGPRs are in close relations with plant roots. They may belong to several bacterial genera such as *Pseudomonas*, *Bacillus*, *Azotobacter*, *Burkholderia*, *Azospirillum*, *Paenibacillus*. Rhizobacteria may enhance plant growth by generating phytoestrogens or by overwhelming pathogen microorganisms [205, 206]. They also produce phytohormones. The six major classes of phytohormone produced by PGPR may induce plant growth, initiate plant immunity, sustain stress tolerance, and support plant maturity for fruiting and seedling [207]. From this point of view, phytohormone-producing PGPR covers the role and significance of sustainable agriculture. Some of them may regulate plant physiology by mimicking the synthesis of plant hormones. Plant-growth-promoting rhizobacteria (PGPRs) cause a series of chemical changes in soil by increasing minerals and nitrogen. They are applied to crops for growth enhancement and disease control [208, 209]. Various stress types of salt, including chilling, nutritional stress, pathogen infection, heat, metals, and wounding, may cause damage to crops [210]. The use of PGPR may affect plant hormone signaling pathways by generating gibberellin, auxins, ABA, and cytokinins or by intervening plant ethylene quantities by forming ACC deaminase reduced the damage to plants that follow in stress situations by definite mechanisms at sites where stress is a chief restriction [211]. Salicylic acid is a significant

plant hormone vital for the immune reaction to pathogens. SA has an essential role in disease resistance signaling [212]. The SA reaction pathway is typically effective against pathogens [213]. SA is a phenolic compound that may be synthesized from the primary metabolite by systemically induced disease resistance responses [214]. Plants are involved in complex signal transduction pathways [215].

Jasmonic acid (JA) is a plant hormone vital for the immune reaction to pathogens. JA was initially isolated from plants of the *Jasminum* spp. and other fruits. It can modulate the ripening of fruits, root growth, pollen production, tendril coiling, and plant resistance to pathogens. JA concentrations in uninduced plant tissues are mostly very minor in plant species [216, 217]. JA biosynthesis is controlled by various elicitors such as wounding [210, 216, 218]. The expressions of numerous genes, with lipoxygenase (LOX) and AOS, were boosted by exogenous application of JA [219–222] and connected with an amplified level of endogenous JA [223, 224].

Ethylene (C₂H₄) is a simple gaseous hydrocarbon that has special effects on plant development and growth [225]. A chief component of resistance signals is constructed thru numerous plant-pathogen interfaces. It is a significant modulator of plant immunity [226–228]. Ethylene has an important potential in the growth of the plant. Although greatest commonly associated with ripening, ethylene is a regulator of seed germination, leaf and petal abscission, seedling growing, stress, organ senescence, and pathogen reactions.

Abscisic acid is a 15-C weak acid that was identified in the early 1960s. It is a development inhibitor amassing in abscising cotton fruit (“abscisin II”) and sycamore trees stimulated to develop dormant (“dormin”) [229–232]. ABA has been adjusting some plant development and growth features such as seed dormancy, embryo maturation, elongation, germination, cell division and floral initiation, and reactions to ecological stresses like cold, drought, salinity, pathogen incident, and UV radiation. The presence of ABA in abscising organs reveals its potential in stimulating senescence and/or stress reaction. Young tissues have great ABA levels, and ABA-deficient mutant plants are highly undersized in part since their capability in reducing transpiration [233]. Recent studies have greatly concentrated on understanding of ABA signaling mechanism [234]. ABA is a significant modulator of the plant immune signaling complex. Besides this, it has an important role in growth and modification to abiotic stress such as salinity and drought stress [235–237]. Plant immunity is suppressed by ABA signaling using the SA-dependent defense mechanism [238–241].

Auxins play an essential role in plant development [242]. Microorganisms may produce auxins or influence auxin signaling in the host [243, 244]. Auxin signaling may suppress SA quantities and signaling [245]. Many pathogens changed ways to achieve auxin-mediated destruction of SA to improve the sensitivity of the host [246].

The GAs encompasses many diterpenoid carboxylic acids, common in higher plants as endogenous development regulators that involve in promoting organ growth and growing variations. These complexes are also constructed by several bacteria, plants, and fungi species. The role of GAs in microorganisms has only lately been researched. Biologically functioning GAs concentration is firmly controlled and is moderated by various developing and environmental signals. The latest investigation has focused on the expression of the genes that encode the dioxygenases plays a role in biosynthesis and inactivation. GAs influence plant development by regulating the deprivation of development inhibitory DELLA proteins [247]. They tightly play a role in plant immune signaling [248]. MAMPs are produced by soil-borne microorganisms [249, 250]. Because of the abundance of soil rhizosphere inhabiting microorganisms, immune signaling in plant roots should be controlled frequently [251]. Hormone-regulated responses may affect the composition of the native microflora of the rhizosphere [252, 253]. Beneficial soil

microorganisms use strategies that rely on hormone-adjusted immune reactions that are activated in the roots on preliminary detection [254].

7. Virus-induced-phytohormone remodeling in plant tissues

Plant hormones ethylene (ET), salicylate (SA), jasmonate (JA), and abscisic acid (ABA) primarily regulate synergistically or antagonistically against pathogens [251]. Plants respond to pathogen invasion by the hypersensitive response (HR), R-mediated, and systemic acquired resistance (SAR). The signaling of systemic acquired resistance (SAR) depends on the discernment of ethylene and salicylic acid [255] synergistically [256] or independently and antagonistically [257]. Phytohormones and precursors, such as salicylic acid (SA) and aminocyclopropane-1-carboxylic acid (ACC), increased antioxidant enzyme activities and defense-associated genes related to SAR [257].

Hypersensitive response of plant cell death reinforces systemic acquired resistance to prevent pathogen movement. The genes are generally associated with plants expressing systemic acquired resistance and hypersensitive response induce ROS (Reactive Oxygen Species) MAP kinase activation, protein phosphorylation, changes in the ion fluxes, and phytohormones as the first responses to stress conditions. The intersection of emerging signals causes reprogramming of defensive metabolites [258, 259]. Integration of abscisic acid (ABA) and salicylic acid (SA) signals resulting from pathogen-related (PR) gene expression during pathogen invasion induce defense mechanism and increase expression of genes associated with resistance [103]. Otherwise, different SA signaling pathway is responsible for PR gene expression independently and related alternative oxidase (AOX) induction [260]. Expression of Cucumber mosaic virus protein cmv2b inhibits SA-mediated resistance by inducibility of AOX (alternative oxidase) [261]. Relationship between AOX and virus resistance, explained by disruption of redox signaling in the mitochondrion [262]. SA modulates the opening of mitochondrial permeability transition pore, and alternative oxidase (AOX) limits the systemic spread of the viruses [263].

Expressed transcriptional factors regulate responsive defense hormone in plants during pathogen invasion. The NAC transcription hormone signals [264] response to pathogen infection as well as to stress conditions. TMV-P0 inoculated, and plant defense-related hormone-treated Capsicum plants overexpress the CaWRKYd gene. Silencing of CaWRKYd affects HR lesion formation [265]. WRKY transcription factors identified as abscisic acid (ABA) signaling regulators. WRKY40 regulates the expression of genes responsible for ABA production and modifies the transcription of numerous defense-related genes.

Callose accumulation and stomatal closure limiting virus movement are the first responses to stress conditions regulated by the plant stress hormone ABA [266]. Exogenous application of ABA increases resistance to tobacco mosaic virus [267] and tobacco necrosis virus infection [268]. The abscisic acid (ABA) acts both resistance and susceptibility side against virus diseases related to different diseases such as Cucumber mosaic virus (CMV) and Bamboo mosaic virus (BaMV) [251]. ABA treatment increases antiviral defense responses of plants and contributes antiviral disease resistance [269]. ABA postponements the multiplication of TMV in invaded leaves and prevents systemic movement. WRKY8 prevents virus infection regulated by ABA signaling enhances immune responses against viruses. Another transcription factor ABA-responsive MYB gene identified from the avian myeloblastosis virus was widely distributed in plants [270]. MYBs interrelate with phytohormones in plant defense against virus disease and serve as a molecular connection to

integrate abscisic acid (ABA) and salicylic acid (SA) signals and enhance disease resistance induction of PR genes during *Pseudomonas syringae* invasion [271]. MYB1 performs in the crosstalk between phytohormones and defense responses to regulate the SA-dependent defense responses against TMV [257].

Ethylene (ET) plays a complex role in resistance against pathogens, and the scheduling of ethylene application affects plant defense against viral infection [251, 257]. ET contributes to virus susceptibility and plays a negative role in anti-TMV-cg defense. Ethylene-mediated MYB4L signaling pathway affects the susceptibility to TMV as a consequence of the SA-independent resistance mechanism [257]. Aminocyclopropane-1-carboxylic acid (ACC) treatment increased the accumulation of TMV-cg systemically [267] and Turnip mosaic virus (TuMV) [272]. On the contrary, ACC, the precursor of ethylene, accumulates around necrotic lesions of TMV-infected plants, and SAR depends on the perception of ethylene [273]. Supplementation of the ACC had a suppressive influence on the replication of the white clover mosaic virus [122]. ACC-pretreatment increases the transcription of MYB4L and stimulates ethylene production during viral infection to enhance TMV resistance [257]. Overexpression of ET-response transcription factor (ERF) enhances resistance to tobacco mosaic virus infection preventing systemic spread of the virus independently exogenous application of salicylic acid, jasmonic acid, or ethylene [274].

Another evidence of phytohormone-mediated resistance to viruses is viral silencing suppressors (VSRs) [261]. VSRs regulate to integrate connections between hormone signaling and subcellular organization [275]. Most viruses encode silencing suppressors (VRSs) to suppress SA-related defense responses [276]. SA-dependent signaling pathway leads the virus resistance [251]. RNA reliant on RNA polymerase (RdRp) open reading frame (ORF) is responsible for RNA silencing suppressors to inhibit SA signaling and ABA [277]. CMV 2b expression inhibits the salicylic acid (SA)-mediated defense response. Virus-encoded suppressor of RNA silencing protein can constrain to overcome SA-mediated resistance mechanism [278]. An exogenous SA application capable of induction RNA silencing antiviral defense response to VSR protein [261]. Systemic movement of ToRSV was reduced with SA pretreatment. SA signaling plays a role restriction of systemic infection but not RNA silencing [279]. Conversely, Alamillo et al. [280] reported that the SA signaling system enriches the function of the RNA silencing system in tobacco. SA-inducible RNA-dependent RNA polymerases (RDRs)-mediated RNA silencing mechanism and the AOX-regulated pathway enhanced resistance to tobamoviruses independent by PR genes [263, 281]. Exogenous SA application suppressed replication of Potato virus Y in tobacco [282], and RNA silencing mechanism associates plant immunity against viral pathogens [283].

Virus spread is commonly limited by the siRNA microRNA system at the transcriptional or post-transcriptional level [251]. The SA-dependent overlaps between hormones and siRNA, miRNA [262, 284], RNA silencing system [256, 262, 284] (Yu et al. 2003), JA-mediated (VSR) proteins [276], CMV-2b-VSR interferes [261] were evidenced in various studies.

ARFs are the key factors in auxin signaling factors that interact with the helicase domain of TMV replicase [285]. TMV replicase-Aux/IAA interactions increase virus pathogenicity in tissues of tomato plants where Aux/IAA proteins accumulate [286]. Repression of the auxin receptor increased rice susceptibility to Rice black-streaked dwarf virus (RBSDV), and Rice stripe virus (RSV) expression of auxin signaling genes changed in response to virus infection [287, 288]. Tobacco mosaic virus (TMV) disrupts auxin/indole acetic acid (Aux/IAA) transcriptional regulators and access to the phloem for systemically spreading [289]. Tomato spotted wilt virus (TSWV) manipulates auxin signaling by interruption of Auxin Response Factor

(ARFs) to optimize their own replication and spread [290, 291]. Viral suppressor HCPro component of Tobacco vein banding mosaic virus (TVBMV) triggers auxin biosynthesis and an increase in auxin accumulation in plants [281].

In the last century, endogenous cytokinins and pathogen interactions in plants propounded [292]. Cytokinin levels confer resistance against White clover mosaic virus [122], Tobacco necrosis virus (TNV) [293], Potato virus Y [294]. Cytokinin may modulate the redox signaling system and trigger defense reactions [278]. Cytokinin accumulation suppresses virus-induced necrotic symptoms and increases ascorbate peroxidase and catalase activities, ascorbate levels, and H₂O₂-scavenging capacity [293]. White Clover Mosaic Potexvirus infection decreases the level of free bases but increases the accumulation of nucleotides. Despite the cytokinin concentration being the same for both control and infected leaves, the distribution of the specific cytokinin groups in the virus-invaded leaves had changed significantly [122].

Researchers interested in the relationship between virus accumulation and gibberellic acid (GA) and the earlier findings demonstrated that virus content was not reduced by GA [295]. However, virus infection affects GA biosynthesis and accumulation. Rice dwarf virus (RDV) infection reduces GA biosynthesis in rice [291], tomato yellow leaf curl Sardinia virus (TYLCSV) in *S. lycopersicum* [296]. Tobacco mosaic virus in tobacco [297] and CMV significantly reduces the content of jasmonic acid (JA), indole acetic acid (IAA), salicylic acid (SA), and gibberellic acid (GA₃) in cucumber plants [298]. Pathogen invasion induces BR biosynthesis and signaling pathways in both resistant and susceptible plants. The resistance against the Rice stripe virus (RSV) can be enhanced by Brassinosteroids (BR) and jasmonic acid (JA) signaling, and RSV invasion is suppressed by the endogenous BR levels [299].

Conflict of interest

The authors declare no conflict of interest.

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