Role of Phytohormones in Plant-Microbial Interaction

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Abstract Plants in their lifetime interact with a wide variety of microbes that can be pathogenic or beneficial. While beneficial microbes can be either endophytes or rhizospheric, pathogenic microbes are mostly free-living and colonize either the phyllosphere or the rhizosphere. These microbes can be either fungi or bacteria and have co-evolved to interact with their host plants using specific mechanisms. Plant-associated microbes release several chemicals onto the surfaces that they colonize, which are known to modulate the biology of the colonized plants directly or indirectly. Plants have evolved to specifically respond to the presence of such microbes, either by gearing up their defence responses (in case of pathogenic microbes) or in a mutually beneficial manner (in case of beneficial microbes). It is but obvious that this relationship between plants and their interacting microbes involves a variety of signalling and metabolic networks, both, from the microbe, as well as the plant side. In this cross-talk between microbes and plants, a very important role is played by phytohormones such as auxins, cytokinins, gibberellins, abscisic acid, jasmonic acid, salicylic acid, ethylene, brassinosteroids etc. Some of these phytohormones are commonly synthesized in the plants and also the plant-associated microbes are known to release some of these phytohormones into their habitat, consequently influencing plant responses. These microbes are also known to impact signalling mechanisms in their host plants by modulating the metabolism of important phytohormones in them. Such modulations in plant phytohormone metabolism have a pleotropic impact on a wide array of metabolic and signalling networks in them, thus affecting, not only their specific responses to the microbes, but also their growth, development and general stress response mechanisms. This chapter highlights the importance of phytohormones in plant–microbe interaction, both in case of pathogenic as well as beneficial microbes.

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1 Introduction

The role of phytohormones in growth, development and stress tolerance/resistance in plants is a very well-studied area of research with a strong history. The metabolism and signalling mechanisms of auxin, cytokinin and gibberellins in plants have been elaborated in the other chapters of this book. In this chapter, we highlight several aspects of phytohormone signalling involved in the interaction between plants and microbes, with special emphasis on the above three phytohormones. Plants, in their lifetime, encounter both, pathogenic as well as beneficial microbes that have co-evolved with their hosts for mutual interaction. These microbes can either be fungi or bacteria. While pathogenic microbes can be both, phyllospheric (colonizing leaf surfaces) and rhizospheric (colonizing rhizosphere/roots), beneficial microbes typically live in the soil and are, therefore, rhizospheric. Rhizospheric microbes can either be free-living or endo-colonizers and are collectively termed as plant growth promoting microbes (PGPM; PGPR for rhizobacteria and PGPF for fungi). Pathogenic microbes can either be biotrophs (need live plant tissues for nutrition) or necrothrophs (live on dead plant tissues), and in either case, can cause extensive damage to plants. Plants have evolved to recognize the presence of pathogens on their surface and respond by recruiting specific defence-related metabolic and signalling pathways that provide them resistance against these pathogens. Beneficial, soil microbes on the other hand co-exist with plants in a mutually beneficial manner, as obligatory or facultative symbionts. They are known to positively impact plant growth, development and stress tolerance/resistance by modulating several metabolic and signalling pathways in plants. It has been well established that there is a substantial amount of cross-talk between plants and the microbes they interact with. Much of this cross-talk is mediated by phytohormones such as auxins, cytokinins, gibberellic acid (GA), abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA), ethylene, brassinosteroids etc. Some of these phytohormones (particularly auxinss, cytokinins and GA) are common growth regulators in both, plants and microbes and are biosynthesized via similar (in some cases, identical) pathways. They are metabolized according to their specific requirements in growth, development and stress mitigation in plants versus bacteria. Plant–microbe interaction with respect to phytohormone signalling works in two ways:

(a) The phytohormones biosynthesized by several of these microbes are released exogenously. For example, several strains of PGPM release these growth hormones into the rhizosphere where they positively modulate the root structure architecture, thus enabling the microbes to efficiently colonize the rhizosphere.
(b) Many of these microbes are known to modulate the endogenous phytohormone metabolism and signaling processes in plants, which enables several aspects of plant responses to these microbes.

Both these phenomena have been discussed in this chapter.

2 Biosynthesis and Metabolism of Phytohormones in Microbes

When cultured in the growth media, many rhizospheric bacteria (harmful and beneficial) are known to produce different phytohormones like auxins, cytokinins, GA and ABA (reviewed by Spaepen and Vanderleyden 2011). Among these microbial-produced phytohormones, auxin is more extensively studied than others. Most soil bacteria produce auxin in the form of indole-3-acetic-acid (IAA) in a tryptophan (precursor for IAA) dependent biosynthetic pathway. The first step involves an enzyme tryptophan mono-oxygenase which converts the amino acid tryptophan into indole-3-pyruvic acid (IPA). Indole-3-pyruvate decarboxylase (IPDC) then converts IPA to IAA (Duca et al. 2014; Patten et al. 2013; Shao et al. 2015). An alternate pathway has also been suggested which involves the conversion of tryptophan to indole-3-acetamide (IA) via the enzyme tryptophan mono-oxygenase followed by conversion of IA to IAA via IA dehydrogenase (Patten et al. 2013; Zupan and Zambryski 1995). Most beneficial bacteria produce auxin via the IPA pathway, while pathogenic (gall/knot forming) soil bacteria commonly use the IA pathway for biosynthesis of IAA. Many bacteria including *Azospirillium* sp., *Enterobacter* sp., and *Pseudomonas* sp., encode the *ipdC* gene responsible for converting indole-3-pyruvic acid to indole-3-acetic acid (Koga et al. 1991; Patten and Glick 2002b; Xie et al. 2005). It has been reported that *iaaM* and *iaaH* genes are involved in IA mediated biosynthesis of IAA in *Pseudomonas fluorescens*, *Erwinia herbicola*, *Erwinia crysanthemi* 3937 and *Ralstonia solanacearum* (Kochar et al. 2011; Yang et al. 2007). A PGPR strain, *Azospirillum brasilense* Yu62 encodes a gene, *aldA* that converts indole-3-acetaldehyde to IAA (suggested as an alternative pathway for IAA biosynthesis in some bacteria). The Pathogenic bacterium *Pseudomonas savastanoi* produces conjugated forms of auxin (responsible for auxin homeostasis in plants) via the *iaaL* gene which encodes the enzyme IAA-lysine synthase, responsible for conjugation of auxin (Glass and Kosuge 1986). These pathways have been summarized in Fig. 1.

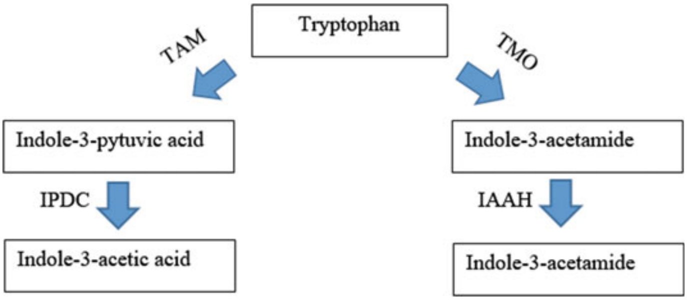

Fig. 1 Commonly used IAA biosynthesis pathway in bacteria. TAM: tryptophan aminotransferase, IPDC: indole-3-pyruvic acid decarboxylase, TMO: tryptophan monooxygenase, IAAH: indole-3-acetamide hydrolase

Apart from auxin, many plant-associated bacteria such as *Agrobacterium tumifaciens*, *Rhodococcus fascians*, *Ralstonia solanacearum* and *Pseudomonas savastonii* etc., are also known to produce the phytohormone cytokinin (Akiyoshi et al. 1989; Barry et al. 1984; MacDonald et al. 1986). The biosynthesis of cytokinin in bacteria generally begins with two isopentenyl transferases (IPT): adenylate-IPT and tRNA-IPT. The transfer of isopentyl group to N6-amino group (prenylation) of the free adenosine nucleotides such as AMP, ADP and ATP or tRNA-bound adenosine phosphate catalyses the first step in cytokinin biosynthesis (Sakakibara 2006; Takei et al. 2001). After prenylation, hydroxylation of isopentyl adenosine nucleotides by cytochrome P450 monooxygenase forms trans-zeatin (tZ). The adenylate, IPT is more commonly found in pathogenic bacteria, and it typically uses adenosine monophosphate (AMP) as a prenyl chain acceptor and dimethylallyl pyrophosphate (DMAPP) and 4-hydroxy-3-methyl-2-enyl pyrophosphate (HMBPP) as prenyl chain donor. The cytokinins are only available as nucleosides incorporated into the tRNA sequence in many bacteria. In most bacteria, tRNA IPT catalyses the formation of isopentyl-ribosides, and the miaA gene encodes the tRNA IPT is present in all bacterial species (except *Mycoplasma* sp.). The tRNA IPT uses both DMAPP and HMBPP as side-chain donors to produce cytokinin (Sakakibara 2006; Takei et al. 2001). While auxin and cytokinin are well studied and characterised in microbes, there are also reports of the production of gibberellic acid (GA) in beneficial growth-promoting bacteria. Most bacteria use geranyl–geranyl diphosphate (GGDP) as the precursor for GA synthesis. Studies conducted by Freiberg et al. (1997) show the presence of GA biosynthetic gene cluster in *Rhizobium* NGR234, a legume colonising bacterium that codes for three cytochrome P450, one geranyl–geranyl diphosphate synthase (GGDPS) and two di-terpene synthases. Also, in *Bradyrhizobium japonicum*, three genes CYP112, CYP114 and CYP117, which encode cytochrome P450 have been identified (Tully et al. 1998).

Similar to bacteria, plant associated fungi also produce phytohormones during their interaction with the host. Many fungi are known to produce phytohormones like auxin, GA and cytokinin (Liao et al. 2018; Pons et al. 2020; Takeda et al. 2015). Similar to bacteria, many fungal species utilize the IPA pathway for biosynthesis of auxin (Kumla et al. 2020). It is well known that one GA was first identified in fungi such as *Fusarium fujikuroi* (Sawada 1912). The biosynthetic pathway for GA in fungi is different from the plants in that it involves the cytochrome P450 gene cluster and GGDP as a precursor similar to the pathway seen earlier in bacteria (Bömke and Tudzynski 2009).

3 Phytohormone-Releasing PGPM and Their Benefits to Plants

It is a well-established fact that PGPM not only biosynthesize phytohormones for their growth and development, but also release them into the rhizosphere. These hormones include auxin, cytokinin, GA, ABA etc. either in free or conjugated forms (Saharan and Nehra 2011; Vacheron et al. 2013; Vejan et al. 2016; Gouda et al. 2018; Numan et al. 2018). This property of PGPM is considered to be a key mechanism in improving plant growth and stress tolerance. For example, it is well established that IAA-producing PGPR are able to increase root surface area in inoculated plants. (reviewed by Mantelin and Touraine 2003). Auxin proding *Bacillus subtilis* LK14 increased plant biomass and chlorophyll content in tomato plants (Khan et al. 2016). Auxin released from the PGPR, *Azospirillum* has has been known to help in imparting abiotic stress tolerance to a variety of crops such as legumes and graminaceous plants (Arzanesh et al. 2011; Cassán et al. 2014). An auxin-overproducing strain of *Pseudomonas putida* GR12-2 has been shown to promot root elongation in canola seedlings (Xie et al. 1996). Similar observations have been reported by Patten and Glick (2002a) in the same strain. *Micrococcus luteus* chp37, a cytokinin producing PGPR improved, both, root and shoot biomass in maize, helping the plants overcome water-stress (Raza and Faisal 2013). Similar observations have been made in the in cytokinin-producing *Bacillus subtilis* strains when inoculated with lettuce (Arkhipova et al. 2007) and *Platycladus orientalis* (Liu et al. 2013). Selvakumar et al. (2018) reported that cytokinin-producing *Citricoccus zhacaiensis* and *Bacillus amyloliquefaciens* had similar impacts on tomato plants. A GA-producing PGPR, *Pseudomonas putida* H-2-3 improved drought tolerance in soyabean (Kang et al. 2014a, b, c). GA and ABA-producing *Azospirillum lipoferum* conferred drought tolerance to maize (Cohen et al. 2009) and GA-producing *Azospirillum brasilense* to wheat (Creus et al. 2004).

In a study by Salomon et al. (2014), inoculation of ABA producing *Bacillus licheniformis* and *Pseudomonas fluorescens* improved growth of grapevine under drought conditions. Sandhya et al. (2009, 2010) have reported the production of a variety of phytohormones in the drought-tolerant PGPR, *Pseudomonas putida* GAP-P45 and imparts drought tolerance to maize and sunflower. Ghosh et al. (2019) later reported that the same strain produces different concentrations of auxin, cytokinin, GA and ABA in the growth medium and imparts drought tolerance to *Arabidopsis thaliana.*

Much like rhizobacteria, several strains of soil fungi are also known to release phytohormones into the culture medium. Species such as *Aspergillus fumigatus* and *Penicillium citrinum* have been known to secrete GA in culture medium (Waqas et al. 2012). Cytokinin produced by fungi is involved in drought and salinity stress through cross-talk with ABA (Ansari et al. 2013). Inoculation with *Penicillium* species during salt stress, promoted shoot growth due to the enhanced secretion of active GAs in cucumber plants (Gupta et al. 2021; Waqas et al. 2012).

4 Precise Roles of Microbe-Derived Phytohormones

What happens to the phytohormones that are released by the soil microbes and how exactly do they help in PGPM-induced growth, development and stress tolerance in plants? Considering the pleotropic role of phytohormones in almost every aspect of plant life-history, it can be hypothesized that the mechanisms involving PGPM-mediated improvement in plant health would involve the uptake and utilization of microbe-derived phytohormones. Some studies involving bacterial mutants have established the importance of microbe-derived phytohormones in such beneficial interactions which is described in greater details later in this chapter. However, precise studies on the uptake and utilization of these phytohormones are missing. We can broadly categorize the effects of these microbe-derived phytohormones on (a) modulation of the rhizosphere/roots and (b) modulation of endogenous signalling networks in the host plants.

5 Role of Microbe-Derived Phytohormones in Modulation of Rhizosphere/Roots

It is believed that phytohormones released by PGPM modulate the rhizosphere which helps in their colonization, however, there are not enough reports to corroborate this hypothesis. There are more reports on the role of microbe-produced exopolysaccharide on root colonization. However, the impact of these phytohormone-producing microbes on modulation of root structure architecture is established (Kudoyarova et al. 2019), pointing to a possible role of these phytohormones on bacterial colonization. Since the roots are the first points of contact of any bacterial exudate and the plant, therefore, the impact of these microbe-derived chemicals on parameters such as primary root length, lateral root length and branching, root hair density etc. is but expected. The role of plant-derived phytohormones on root growth and development is well established. It is a well-known fact that the two primary hormones responsible for regulating root growth are auxin and cytokinin. Classical studies have proven that auxin induces lateral root growth in plants, while, both auxin and cytokinin can become inhibitory towards root growth at relatively higher concentrations (Taiz et al. 2015). There are several reports on the impact of phytohormone-producing bacteria on root growth and development, however, there are very few reports establishing a direct correlation between microbe derived phytohormones and root growth or root structure architecture. Nonetheless, based on the roles of phytohormones such as auxin and cytokinin on root growth and architecture, some speculative correlations can be made. For example, it has been seen that auxin or cytokinin-releasing PGPR induce increase in root hair density and lateral root length while, in some cases, inhibition of primary root length has been observed (Shah et al. 2016; Ghosh et al. 2017; Kudoyarova et al. 2019). There are also reports on enhancement of the total root surface by these microbes. It is obvious that many of these changes can lead to increased mineral uptake by roots, thereby increasing root exudation and, possibly, facilitating PGPM colonization The role of auxin and cytokinin producing bacteria on several aspects of root development has been comprehensively reviewed by Kudoyarova et al. (2019). According to this review, the impact of these bacteria on root development is two-fold; a positive impact by some strains and a negative impact by others. The negative impact has been correlated with the inhibitory roles of higher concentrations of auxin and cytokinin on root growth. For example, an increase in root biomass and endogenous root auxin levels were observed in wheat plants inoculated with auxin-producing *Paenibacillus illinoisensis* IB 1087 and *Pseudomonas extremaustralis* IB-K13-1A (Kudoyarova et al. 2017). Similar observations have been reported in wheat inoculated with the salt tolerant PGPR *Pseudomomas moraviensis* (Ul Hassan and Bano 2019) and *Azospirillum* (Dobbelaere et al. 1999). Similarly, drought mitigation in wheat due to enhanced root growth and lateral root formation by auxin producing *Azospirillum* was reported by Arzanesh et al. (2011). Changes in the root architecture due to the production of IAA by PGPR was found in the studies of Mantelin and Touraine (2003), helping the plants in rapid uptake of water from the soil under drought conditions. A beneficial species of fungi, *Trichoderma virens*, inoculated onto *Arabidopsis thaliana*, changed root architecture by modulating IAA concentration (Contreras-Cornejo et al. 2009). There are reports that mutant strains deficient in IAA production were impaired in the type of root growth promotion that the wild type strain could impart. For example, IAA-deficient mutants of *Pseudomomas putida* whose impact was studied on root growth in canola (*Brassica napus*) (Patten and Glick 2002b). Studies with mutants altered in IAA production and their role in modulating root structure architecture in plants has been reviewed by Spaepen and Vanderleyden (2011).

In case of cytokinin producing microbes, *Bacillus amyloliquefaciens* UCMB5113 inhibited primary root growth in *Arabidopsis thaliana* (Asari et al. 2017). This observation was correlated with, both, bacterial cytokinin production which increased root cytokinin levels or the increased auxin levels that were also detected in colonized roots (Asari et al. 2017). Similar changes in root growth in *Arabidopsis thaliana* by phytohormone producing, abiotic stress mitigating soil bacteria has been reported with *Pseudomonas putida* GAP-P45 (Ghosh et al. 2017) and with *Pseudomonas putida* AKMP7 (Shah et al. 2016). These studies reported a reduction in primary root length of Arabidopsis plants under water-stress conditions, when inoculated with the aforementioned strains of bacteria. While, in the former study (i.e., Ghosh et al. 2017), bacterial inoculation was positively corelated with water-stress tolerance, in the later (Shah et al. 2016), water-stress mediated deterioration was observed in plants inoculated with AKMP7.

6 Impact of PGPM on Plant Phytohormone Metabolism and Signalling

An important aspect of plant-PGPM interaction is the widely reported phenomenon of modulation in plant phytohormone levels and metabolism by PGPM. However, the precise mechanism leading to such modulations of endogenous phytohormone levels in plants by PGPM is not clearly understood. Form the current status of research, it can be hypothesized that this may be a key mechanism in PGPM-mediated stress amelioration in plants (Barnawal et al. 2017; Dodd et al. 2010). However, whether these modulations occur due to uptake of bacterial phytohormones by plants or due to alteration in plant's endogenous hormone metabolism induced by bacteria, or a combination of both, remains unclear. Modulations in plant phytohormone levels have been seen in general growth and development as well as stress amelioration processes when inoculated with PGPM. For example, Marulanda et al. (2009) reported an increase in IAA concentration in clover, inoculated with *Pseudomonas putida* and *Bacillus megaterium*. This was positively correlated with enhanced plant biomass. In another study, Kang et al. (2014a) reported increased levels of endogenous GAs in cucumber plants inoculated with PGPR strains like *Burkholdera cepacia SE4*, *Promicromonospora* spp. SE188 and *Acinetobacter calcoaceticus* SE370. *Aeromonas punctata* PNS-1, *Serratia marcescens* 90–166 and *Azospirillum brasilense* Sp245 are PGPR strains capable of producing auxin and inoculation of these bacteria increased the endogenous levels of auxin (Iqbal and Hasnain 2013; Shi et al. 2010). Endogenous levels of IAA in the roots of plants inoculated with *Phyllobacterium brassicacearum* STM196 and *Bacillus* sp. LZR216 were higher than the control plants with concomitant increase in expression of genes involved in IAA biosynthesis (Contesto et al. 2010). Apart from its effects on biosynthesis of phytohormones, PGPR can also affect the transport of endogenous auxin by altering the expression of auxin transporters which can also regulate the growth stimulating activities. For example, inoculation with *Bacillus* sp. LZR216 decreased the synthesis of PIN and AUX (auxin transporters). On the other hand, PIN2 and PIN3 expression is elevated in plants inoculated with *Bacillus phytofirmans* PsJN and mutation in pin2 impacts negatively on the growth promotion by these *Bacillus* species (Poupin et al. 2016; Wang et al. 2015). Certain substances with auxin-like activity produced by PGPR can also affect the endogenous auxin levels. For example, cyclopeptides produced by mutant *Pseudomonas aeruginosa* exhibit auxin-like activity weakly which enhance the lateral root formation and growth compared to the wild-type *Pseudomonas* that are not capable of producing the cyclopeptides (Ortiz-Castro et al. 2011). In-vitro studies using *Arabidopsis thaliana* have shown that volatiles such as acetoin and 3,4-butanediol produced by *Bacillus subtilis* GB03and *Bacillus amyloliquefaciens* IN937a alter endogenous auxin levels with increased expression of auxin biosynthetic genes and they also influence the expression levels of IAA transporter genes (Ryu et al. 2003; Zhang et al. 2007).

Several PGPR strains are capable of synthesizing cytokinin as well as altering the endogenous levels of cytokinin in their host plants (Tsukanova et al. 2017). For instance, elevated levels of endogenous cytokinin were observed in six-week-old *Arabidopsis thaliana* upon seed bacterization with *Burkholderia phytofirmans* PsJN (Su et al. 2016). Exposure of tomato plants to volatiles emitted by *Bacillus subtilis* SYST2 enhanced the expression of cytokinin biosynthetic gene (*Sl*CKX1) and endogenous cytokinin levels. Inoculation of *Bacillus subtilis* (AE016877) increased the endogenous cytokinin levels of *Platycladus orientalis* plants by 97.10% compared to its respective control (Liu et al. 2013). Similarly, PGPM inoculation can affect the endogenous levels of GAs in plants (Tsukanova et al. 2017). Studies using mutant rice plants impaired in biosynthesis of gibberellins shows that PGPR *Leifsonia soli* SE134 and *Enterococcus faecium* LKE12 capable of producing gibberellins can compensate the shoot growth compared to its control (Kang et al. 2014b; Lee et al. 2015). There are certain strains which do not synthesize gibberellins but are capable of elevating the gene expression of GA biosynthetic genes. For instance, *Burkholderia phytofirmans* PsJN increases the expression of *At*GA3ox1which is involved gibberellin synthesis in *Arabidopsis thaliana* (Poupin et al. 2013).

It has been reported that several species of stress-mitigating PGPM are known to modulate phytohormone metabolism and homeostasis in the plants exposed to one or more of these stresses. Environmental stress on plants can broadly be classified into abiotic and biotic stresses. Stress tolerant PGPM are known to help plants in amelioration of both these stresses. There is a substantial body of work on the positive impact of stress-tolerant PGPR on abiotic stress (drought, salinity, thermal stress etc.) tolerance in plants. As far as the role of PGPR in amelioration of biotic stress is concerned, they are mostly helpful in limiting the growth of soil pathogens by a variety of mechanisms, thus earning them the title of "biocontrol" agents. With respect to phythormone signalling, auxin, GA, cytokinin and ABA are considered important for PGPM-mediated abiotic stress tolerance, while SA, JA and ethylene signalling are considered to be important for the phenomenon of biocontrol.

Pereyra et al. (2012) have observed that, on inoculation of wheat seedlings with *Azospirillum* under osmotic stress, there were some morphological changes in the xylem architecture which was due to the upregulation of indole-3-pyruvate decarboxylase gene and increased IAA production in the plants. Enhanced tomerance of cucumber plants to salinity and drought waas positively correlated with endogenous GA levels when inoculated with *Burkholdera cepacia SE4*, *Promicromonospora* spp. *SE188* and *Acinetobacter calcoaceticus SE370* (Kang et al. 2014a). *Phyllobacterium brassicacearum* STM196 has been reported to modulate internal hormonal signaling in *Arabidopsis thaliana* (Contesto et al. 2010; Galland et al. 2012; Bresson et al. 2013). Ghosh et al. (2019) observed that when *Arabidopsis thaliana* plants were inoculated with the IAA and cytokinin producing PGPR *Pseudomonas putida* GAP-P45, the levels of the four major phytohormones-auxin (IAA), cytokinin (Tz), GA and ABA were differently modulated in the roots versus shoots. *P. putida* GAP-P45 downregulated endogenous ABA levels in *Arabidopsis thaliana* under water -stress, while elevating IAA and tZ accumulation in shoots and roots. This bacterium caused an increase in endogenous GA content in shoot but decrease of the same in root tissue of the plants under water-stress was observed. A beneficial species of fungus, *Trichoderma virens* caused alterations in root structure architecture of *Arabidopsis* *thaliana*, by modulating IAA concentration (Contreras-Cornejo et al. 2009). The beneficial fungus, *Piriformospora indica* has been reported to alleviate drought and salinity stress in several plants by secretion of the phytohormone cytokinin and its cross-talk with plant ABA levels (Ansari et al. 2013).

7 Hormonal Signaling in Plant-Pathogen Interaction

In the last two decades, the role of phytohormone signalling in plant-pathogen interaction has been widely explored. Apart from the classical growth hormones elaborated above, exciting research around the world has extended that repertoire to include salicylic acid (SA), jasmonic acid (JA), nitric oxide (NO), strigolactones, karrikins etc. Some pathogens may directly secrete hormones or cause alteration of hormone levels and signalling components to overcome host defence responses with a combination of effectors and interference mechanisms to manipulate available host resources to their advantage (Bari and Jones 2009; Berens et al. 2017). Thus, the nature and magnitude of these interactions determine the overall outcome of host-microbial interactions. On the other hand, application of the hormones can be used to alter plant–microbe interactions directly or by interference in signalling to assess synergistic responses that enhance plant productivity as well as defense responses (Delaney et al. 1994; Li et al. 1996; Tjamos et al. 2005; Johansson et al. 2006). Therefore, a better understanding of plant hormonal responses to pathogens during susceptible and resistant interactions will aid in the effective management of plant diseases while maintaining crop yields. This part of the chapter examines historical and novel developments on plant hormonal changes in response to various pathogens in general. We present a brief overview of the known host genetic components, defense strategies, and molecular mechanisms underlying defense responses about hormone signalling pathways and identify research areas for the future. While the main focus of this chapter is on the roles of auxin, cytokinin and GA signalling, the major hormones impacting plant -pathogen interaction are SA, JA and ethylene. Hence, we first review the roles of these hormones and then move on to the others.

8 Role of Salicylic Acid (SA), Jasmonic Acid (JA), and Ethylene (ET) Signaling in Plant Defense

Salicylic acid (SA) is a plant hormone that plays a central role in plant defense response to pathogens, not only locally, but also during systemic defense response (SAR) in the face of a challenge from multiple pathogens (Delaney et al. 1994; Cao et al. 1997). SA-mediated defense responses are most effective against biotrophic and hemibiotrophic pathogens with a diminished role against necrotrophic pathogens (Glazebrook 2005). In plants, pathogen infection induces biosynthesis of SA mainly through the upregulation of the SA biosynthetic *Isochroismate Synthase 1/Salicyclic Acid Induction Deficient* (*SID2*) gene from the precursor chorismate, which is synthesized in the chloroplast. This induces downstream responses like the production of reactive oxygen species (ROS), hypersensitive response (HR), lignification of the cell wall, production of secondary metabolites like antimicrobials, etc. Interestingly, pretreatment of plants with SA induces resistance to various pathogens (Gong et al. 2017), while plants expressing the *Pseudomonas putida NahG* (encoding the enzyme salicylate hydroxylase that converts SA to catechol) resulted in increased susceptibility to pathogens (Liu et al. 2014; Zheng et al. 2019). Activation of SA mediated defense responses by applying beneficial microbes, including the rhizosphere endophytic PGPR strain *Paenibacillus alvei* K165 to increase resistance in the host plants (Tjamos et al. 2005). Furthermore, transcriptional reprogramming following pathogen infection has been shown to involve SA signaling with various pathogens employing effector molecules to infect the host plant by altering hormone signaling as an infection strategy (Bari and Jones 2009). *Verticillium dahliae Isochorismate synthase* (*VdIsc1*) is one such effector protein employed by the pathogen to suppress SA levels in the host during early infection stages (Liu et al. 2014). When cotton plants were inoculated with a *VdIsc1* deletion mutant, the host SA and SAG levels and the SA marker, *PR1*, were significantly up-regulated. Other pathogen effectors like *VdSCP41* target the master immune regulators *calmodulin-binding protein 60-like g* (*CBP60g*) and *SAR Deficient 1* (*SARD1*), which in turn regulate the defense responses in multiple plant species by binding directly to the promoters of SA signaling components (Qin et al. 2018). Thus, SA signaling plays a significant role during plant-microbial interactions with SA perception, and microbe-mediated alterations of the host SA levels determine the host resistance mechanisms to various pathogenic and beneficial microbes in general.

Another class of plant hormones that plays an important role in multiple processes like biotic stress, abiotic stresses, and plant development includes the jasmonates and jasmonic acid (JA), structurally similar to the metazoan prostaglandins (Chini et al. 2007). In plants, JA is synthesized in chloroplasts through the octadecanoid pathway and is indispensable for resistance against various pests, including herbivory, insects, and necrotrophs, as well as in plant reproduction, including pollen fertility (Xie et al. 1998; Berens et al. 2017). Though the JA signaling pathway genes are activated quickly in response to this pathogen, the levels of active JA and JA-Ile are noticeable at a later stage in the progression of the disease, indicating an active role for the hormone in fungal defense response. Moreover, JA pathway mutants (like *jar1*, *coi1*, and *cyp94B3*) exhibit increased fungal resistance with reduced tissue colonization and lower fungal biomass in roots (Scholz et al. 2018). Lignin polymerization, which is involved in such resistance responses during fungal infection, has been reported to be induced by pathogen infection in a manner involving JA signalling leading to increased resistance in mutants defective in the lignin polymerization enzyme laccase1 (Hu et al. 2018, 2019). Enhancement of JA signalling through involving a negative regulator of JA signaling *Homeodomain Transcription Factor 1* (*HDTF1*) has been linked to increased resistance of cotton to *V. dahliae* and *Botrytis cinerea* (Gao et al. 2016). Other transcriptional regulators like the plant-specific homeodomain-leucine zipper (HD-ZIP) family protein HB12 and the plant-specific NAC transcription family member ATAF1 are involved in the negative regulation of JA mediated defense responses (He et al. 2016, 2018a, b), underscoring the fact that transcriptional reprogramming during defense responses to pathogen actively involves JA mediated signal responses. JA signaling pathway is activated upon fungal infection in a manner that requires stearoyl acyl-carrier-protein desaturase (*SSI2*), leading to activation of defense responses and heightened resistance (Gao et al. 2013a, b). JA signaling pathway has also been linked to pathogen resistance responses through the mediator complex that comprises the conserved multiprotein cofactor of RNA polymerase II and regulates transcription through 20–30 subunits that form four mediator subcomplexes. This complex communicates with hormone signaling to influence multiple plant processes like development, flowering, noncoding RNA processing, secondary metabolism, and defense response to various abiotic and biotic stresses (An and Mou 2013; Li et al. 2018). Multiple studies have shown that the absence of JA leads to the activation of SA-mediated response for resistance against pathogenic fungal infection (Johansson et al. 2006), while pretreatment of plants with JA before subsequent infection leads to resistance against this fungal pathogen by activating basal defense responses (Johansson et al. 2006; Gao et al. 2013a). Though the JA signaling pathway genes are activated quickly in response to this pathogen, the active JA and JA-Ile levels show noticeable changes in only the later part of pathogen infection. Thus, pretreatment of plants with JA before subsequent infection leads to resistance against this fungal pathogen by activating basal defense responses (Johansson et al. 2006; Gao et al. 2013a). Reciprocal regulation of JA-SA mediated defense responses has been observed during the Verticillium wilt of plants (Li et al. 2014).

Ethylene (ET) is a gaseous plant hormone usually associated with senescence and cell death processes in plants which manifest as chlorosis/yellowing of the foliage from the loss of chlorophyll. Necrotrophic pathogen infection in plants results in similar cell death processes leading to the establishment and successful propagation of the pathogen. Thus, it is not surprising that plant defense response to necrotrophic pathogens has been shown to extensively involve ethylene signaling (Broekaert et al. 2006), with evidence of increased ET levels coinciding with the onset of disease symptoms (Cronshaw and Pegg 1976). The ethylene biosynthetic enzyme 1-aminocyclopropane-1-carboxylate synthase (*ACS6*) has been reported to be induced upon pathogen infection, further confirming the role of ethylene during pathogen infection (Wang et al. 2004; Zhou et al. 2012). Increased ethylene production has been observed in susceptible cultivars than tolerant potato cultivars upon exposure to fungal culture filtrate and toxin. At the same time, inhibition of the host ET signaling abrogated this toxin-induced and ET-mediated symptom development in the host (Mansoori and Smith 2005). Ethylene production followed pathogen infection, and ET signaling components are required for defense response against fungal pathogens. In contrast, treatment of the pathogen-challenged host with the ethylene precursor molecule 1-aminocyclopropane-1-carboxylic acid (ACC) resulted in increased host resistance underlined by increased fresh weight of the inoculated plants (Johansson et al. 2006). Interestingly, silencing of the ET receptor genes *Never*

Ripe (*SlNr*) and *SlETR4* resulted in reduced disease incidence, severity, and reduced fungal biomass indicative of enhanced resistance to fungal infection (Pantelides et al. 2010a). Pathogen resistance through lignification of the cell-wall also involves ET signaling with *Ethylene Response Factor-like* gene (*ERF1 like*) and *Ethylene Response Factor 6* (*GhERF6*) transcription factors shown to bind to the GCC-box element in the promoters of the defense-related genes and positively regulate defense against fungal pathogens (Guo et al. 2016; Yang et al. 2015). However, the role of ET during fungal infection has been contradictory, with some studies indicating a dual role for ET in resistance and the promotion of wilt. In this context, it is interesting to note that impaired perception of ET in the *Arabidopsis etr1-1* mutant led to a significant reduction in pathogen growth and increased resistance during Verticillium wilt ET, with a similar result achieved upon application of the ET inhibitor aminoethoxy vinyl glycine (AVG) either before or at the time of inoculation (Pantelides et al. 2010b; Robison et al. 2001a). On the other hand, plants transformed with a catabolic enzyme—the bacterial *ACC deaminase* gene under root-specific to inhibit ET synthesis, significantly reduced or delayed disease symptoms by targeted degradation of the ET precursor ACC, resulting in an overall reduction of disease symptoms (Robison et al. 2001b). Such dual nature of ET signaling can be explained by the fact that initial perception of the pathogen may be activating ET signaling and ET biosynthesis at the site of infection to limit the spread of the pathogen, but once the pathogen has already been established in a host, it might aid in the establishment of the necrotrophic phase of the pathogen.

9 Role of Cytokinin (CK), Auxin (AUX), Gibberellic Acid (GA), Brassinosteroid (BR), Nitric Oxide (NO), and ß-Aminobutyric Acid (BABA) in Pathogen Resistance

A decrease in the cytokinin levels in the tracheal fluid and the above-ground tissue in cotton plants and tomato plants treated with a pathogenic strain of *Verticillium* spp. in symptom development has been reported (Misaghi et al. 1972; Patrick et al. 1977). A decrease in water potential in the root leading to a reduction in CK levels has been proposed to underline the visible yellowing of the leaves due to chlorosis and loss of pigments during Verticillium wilt (Patrick et al. 1977). Up-regulation of cytokinin degrading enzymes leading to a decrease in the host cytokinin levels, particularly trans-zeatin [tZ], has been documented to concur with *Verticillium*-induced premature senescence (Reusche et al. 2013). Taken together, these results indicate that reduced cytokinin levels most likely promote infection caused by a necrotrophic pathogen or during the necrotrophic phase in the life cycle of a pathogen laying the framework for efficient colonization of the host leaves by active induction of senescence (Reusche et al. 2013). This is supported by the fact that external application of synthetic cytokinins and inhibition of the cytokinin degrading enzymatic activity led to reduced symptoms and proliferation of the fungus on the host (Reusche et al. 2013). Thus, cytokinin levels seem to play a role during plant defense responses to specific pathogens that promote senescence as a strategy for enhancing pathogenicity on susceptible hosts.

Many microbes produce/secrete bioactive molecules, including hormones as secondary metabolites, including the model bacterial pathogen *Pseudomonas syringae* and the fungal pathogen *Verticillium dahliae*. Recent work has shown that volatile compounds (VCs) from *Verticillium* spp. cause preferential allocation of resources driving the root growth over shoot growth by manipulating auxin (AUX) signaling pathways in the host plant. Various approaches, including chemical inhibition of the AUX signaling pathway using an auxin efflux inhibitor, compromised this change in growth pattern, further underscoring the role of AUX during pathogen infection. Indeed, several components of the AUX signaling pathway, including *TIR1*, *TIR3*, *AUX1*, and *AXR1*, were subsequently shown to be involved in the regulation of resistance to both fungal and bacterial pathogens in the host plants (Li et al. 2018).

GA signalling has been shown to be involved in a few instances of disease pathology, including the bakanae disease on rice (Studt et al. 2013) and during the infection by rice dwarf virus (Zhu et al. 2005). In this regard, the DELLA proteins that negatively regulate the GA signaling pathway involved in plant growth are fast emerging as plant defense response regulators that balance plant growth during biotic and abiotic stress (Hou et al. 2010). Recent work has shown that increased bioactive GA through induction of GA biosynthetic genes combined with suppression of *DELLA* genes contribute to hyper GA signaling seems to increase the susceptibility of the defense compromised *ndr1-1* mutant in *Arabidopsis* while promoting a faster transition to flowering in response to pathogen infection (Dhar et al. 2019).

A class of steroid hormones that are found in both plants and animals includes the recently discovered brassinosteroids (BR) is perceived by cell surface receptors in plants in contrast to that found in the animal counterpart and is primarily involved in plant growth, development, cell differentiation, and photomorphogenesis (Wang et al. 2012). However, a role for BR signaling in plant defense is starting to emerge, with its role in balancing defense and development attracting further attention. Epibrassinolide treatment in longer-term seemed to positively regulate resistance to fungal pathogen in tomato and cotton while activating the JA signaling pathway (Krishna 2003; Gao et al. 2013b; Roos et al. 2014; Bibi et al. 2017). Studies have shown that both pathogen infection and epibrassinolide significantly elevated the level of the enzymes involved in carbohydrate metabolism, including sucrose phosphate synthase (SPS), vacuolar/cell wall-bound acid invertase (AI), and cytosolic sucrose synthase (SuSy), helping to negate the pathogen-induced osmotic stress in the host, thus contributing to host resistance (Goicoechea et al. 2000; Bibi et al. 2014). Various components of BR signaling, including *BAK1* that encodes an LRR-RLK associated with the BR receptor *Brassinosteroid Insensitive 1* (*BRI1*), is required for resistance against the fungus in multiple species (Fradin et al. 2009; Gao et al. 2013a; Roos et al. 2014). Yet another RLK *Suppressor of BIR1* (*SOBIR1*) that is associated *BAK1-interacting receptor-like-kinase 1* (*BIR1*) and hence an integral component of BR signaling in plants is required for resistance against various pathogens and regulates plant defense responses through its interaction with multiple receptor-like proteins (RLPs) (Liebrand et al. 2013; Zhou et al. 2019). Taken together, these findings suggest that BR signalling might play a more significant role in plant defense response than previously expected for a hormone that initially came to prominence for its primary involvement in plant growth and development.

Recently the gaseous hormone nitric oxide (NO) has been implicated in ROS and defense signalling in plants. *Verticillium* infection and *Vd* toxins have been known to induce cell death with the active involvement of ROS (Jia et al. 2007), while *Vd* toxin alters hormone balances during *Verticillium* infection (Pegg and Brady 2002). However, both NO and H_2O_2 are produced in cotton suspension cells treated with *Vd* toxin have been known to produce both NO and H_2O_2, with the upregulation of defense associated redox proteins glutathione S-transferases (GSTs) proteins associated with the NO signaling pathway (Jia et al. 2007). Leaves of *Arabidopsis* plants treated with the *Vd* toxin produce NO with peak activity around an hour post-treatment which is abrogated in the NR deficient *nia1 x nia2* mutant (Shi and Li 2008). Additionally, the *Vd* toxin-induced NO production results in the depolymerization and destabilization of the cortical microtubules rather than the actin microfilaments inside the cell, resulting in HR-like cell death along with the activation of the host defense responses (Shi et al. 2009). Yet another study with *Vd* toxins and mutant analysis has shown that H_2O_2 functions upstream of NO as a result of modulation of dynamic microtubule cytoskeleton through the blockage of NO production, mediated by nitrate reductase, leading to activation of defense against the fungal pathogen *V. dahliae* infection (Yao et al. 2012). Further work has shown that the downregulation of defense-related SA and NO hormone levels in the VIGS-mediated silencing of the coiled-coil (CC)–NBS–LRR-type gene (*GbRVd*) in cotton predisposes them to be susceptibility against *Verticillium* infection (Yang et al. 2016).

Yet another active chemical, ß-aminobutyric acid (BABA), emerging as a novel plant growth regulator, has been shown to induce resistance to various pathogens. It prevents disease symptoms, including stunting of plants during Verticillium wilt of the oilseed rape by activating higher synthesis and accumulation of phenylpropanoids (Kamble et al. 2013). This heightened resistance is underlined by a change in vascular architecture and storage of resistance-enhancing phenolics, leading to the containment of the pathogen by inhibiting colonization of the shoot (Kamble et al. 2013).

10 How Indispensable Are Microbe-Derived Phytohormones for Plant Responses to Microbes?

As described above, phytohormones play a key role in the interaction between plants and associated microbes, whether beneficial or pathogenic. Both plants and microbes biosynthesize phytohormones and several microbes release them into their colonizing habitats. These phytohormones and other chemicals released by the microbes modulate the endogenous metabolic and signaling networks within the plant, thus impacting the way they respond to the presence of microbes in their vicinity. As described above, several studies involving plant and microbial mutants have identified the importance of microbe-derived phytohormones in plant responses to their associated microbiota. While these studies help establish the connection between plant and microbial phytohormone signaling networks, further studies need to be done to understand the precise mechanisms underlying the responses of plants to microbe-derived phytohormones. However, it is clear now that the different classes of plant hormones not only have specific roles in impacting plant physiology, development and stress tolerance, but with accumulating evidence, they also seem to help plants in interacting with their biotic environment. Thus, phytohormone based signalling mechanisms between plants and associated microbiota are intricately interconnected, sharing multiple pathway components with overlapping functions to maintain a well-oiled cellular machinery that helps the sessile organisms in deriving benefit from soil microbiota and safe-guarding them from the continuous barrage of omnipresent pathogenic microbes in nature.

References

Akiyoshi DE, Regier DA, Gordon MP (1989) Nucleotide sequence of the tzs gene from *Pseudomonas solanacearum* strain K60. Nucleic Acids Res. https://doi.org/10.1093/nar/17.21.8886

An C, Mou Z (2013) The function of the Mediator complex in plant immunity. Plant Signal Behav 8(3):e23182. https://doi.org/10.4161/psb.23182

Ansari MW, Trivedi DK, Sahoo RK, Gill SS, Tuteja N (2013) A critical review on fungi mediated plant responses with special emphasis to *Piriformospora indica* on improved production and protection of crops. Plant Physiol Biochem 70:403–410. https://doi.org/10.1016/J.PLAPHY.2013.06.005

Arkhipova TN, Prinsen E, Veselov SU, Martinenko EV, Melentiev AI, Kudoyarova GR (2007) Cytokinin producing bacteria enhance plant growth in drying soil. Plant Soil 292(1–2):305–315. https://doi.org/10.1007/s11104-007-9233-5

Arzanesh MH, Alikhani HA, Khavazi K, Rahimian HA, Miransari M (2011) Wheat (*Triticum aestivum* L.) growth enhancement by *Azospirillum* sp. under drought stress. World J Microbiol Biotechnol 27(2):197–205. https://doi.org/10.1007/s11274-010-0444-1

Asari S, Tarkowská D, Rolčík J, Novák O, Palmero DV, Bejai S, Meijer J (2017) Analysis of plant growth-promoting properties of Bacillus amyloliquefaciens UCMB5113 using *Arabidopsis thaliana* as host plant. Planta 245(1). https://doi.org/10.1007/s00425-016-2580-9

Bari R, Jones JD (2009) Role of plant hormones in plant defense responses. Plant Mol Biol 53:412–428. https://doi.org/10.1007/s11103-008-9435-0

Barnawal D, Bharti N, Pandey SS, Pandey A, Chanotiya CS, Kalra A (2017) Plant growth-promoting rhizobacteria enhance wheat salt and drought stress tolerance by altering endogenous phytohormone levels and *TaCTR1* / *TaDREB2* expression. Physiol Plant 161(4):502–514. https://doi.org/10.1111/ppl.12614

Barry GF, Rogers SG, Fraley RT, Brand L (1984) Identification of a cloned cytokinin biosynthetic gene. Proc Natl Acad Sci. https://doi.org/10.1073/pnas.81.15.4776

Berens ML, Berry HM, Mine A, Argueso CT, Tsuda K (2017) Evolution of hormone signaling networks in plant defense. Ann Rev Phytopathol 55:401–425. https://doi.org/10.1146/annurev-phyto-080516-035544

Bibi N, Fan K, Dawood M, Nawaz G, Yuan SN, Wang XD (2014) Exogenous application of epibrassinolide attenuated *Verticillium* wilt in upland cotton by modulating the carbohydrates metabolism, plasma membrane ATPases and intracellular osmolytes. Plant Growth Regul 73:155–164. https://doi.org/10.1007/s10725-013-9877-5

Bibi N, Ahmed IM, Fan K, Dawood M, Li F, Yuan S et al (2017) Role of brassinosteroids in alleviating toxin-induced stress of *Verticillium dahliae* on cotton callus growth. Environ Sci Pollut Res Int 24:12281–12292. https://doi.org/10.1007/s11356-017-8738-6

Bömke C, Tudzynski B (2009) Diversity, regulation, and evolution of the gibberellin biosynthetic pathway in fungi compared to plants and bacteria. Phytochemistry. https://doi.org/10.1016/j.phytochem.2009.05.020

Bresson J, Varoquaux F, Bontpart T, Touraine B, Vile D (2013) The PGPR strain *Phyllobacterium brassicacearum* STM196 induces a reproductive delay and physiological changes that result in improved drought tolerance in *Arabidopsis*. New Phytol 200(2):558–569. https://doi.org/10.1111/nph.12383

Broekaert WF, Delaure SL, De Bolle MF, Cammue BP (2006) The role of ethylene in host pathogen interactions. Ann Rev Phytopathol 44:393–416. https://doi.org/10.1146/annurev.phyto.44.070505.143440

Cao H, Glazebrook J, Clarke JD, Volko S, Dong X (1997) The *Arabidopsis NPR1* gene that controls systemic acquired resistance encodes a novel protein containing ankyrin repeats. Cell 88:57–63. https://doi.org/10.1016/S0092-8674(00)81858-9

Cassán F, Vanderleyden J, Spaepen S (2014) Physiological and agronomical aspects of phytohormone production by model plant-growth-promoting rhizobacteria (PGPR) belonging to the genus *Azospirillum*. J Plant Growth Regul 33(2). https://doi.org/10.1007/s00344-013-9362-4

Chini A, Fonseca S, Fernandez G, Adie B, Chico JM, Lorenzo O et al (2007) The JAZ family of repressors is the missing link in JA signaling. Nature 448:666–671. https://doi.org/10.1038/nature06006

Cohen AC, Travaglia CN, Bottini R, Piccoli PN (2009) Participation of abscisic acid and gibberellins produced by endophytic *Azospirillum* in the alleviation of drought effects in maize. Botany 87(5):455–462. https://doi.org/10.1139/B09-023

Contesto C, Milesi S, Mantelin S, Zancarini A, Desbrosses G, Varoquaux F, Bellini C, Kowalczyk M, Touraine B (2010) The auxin-signaling pathway is required for the lateral root response of *Arabidopsis* to the rhizobacterium *Phyllobacterium brassicacearum*. Planta 232(6):1455–1470. https://doi.org/10.1007/s00425-010-1264-0

Contreras-Cornejo HA, Macías-Rodríguez L, Cortés-Penagos C, López-Bucio J (2009) Trichoderma virens, a plant beneficial fungus, enhances biomass production and promotes lateral root growth through an auxin-dependent mechanism in *Arabidopsis*. Plant Physiol 149(3):1579–1592. https://doi.org/10.1104/pp.108.130369

Creus CM, Sueldo RJ, Barassi CA (2004) Water relations and yield in *Azospirillum*-inoculated wheat exposed to drought in the field. Can J Bot 82(2):273–281. https://doi.org/10.1139/b03-119

Cronshaw DK, Pegg GF (1976) Ethylene as a toxin synergist in *Verticillium* wilt of tomato. Physiol Plant Pathol 9:33–34. https://doi.org/10.1016/0048-4059(76)90073-4

de Jonge R, van Esse HP, Maruthachalam K, Bolton MD, Santhanam P, Saber MK et al (2012) Tomato immune receptor *Ve1* recognizes effector of multiple fungal pathogens uncovered by genome and RNA sequencing. Proc Natl Acad Sci USA 109:5110–5115. https://doi.org/10.1073/pnas.1119623109

Delaney TP, Uknes S, Vernooij B, Friedrich L, Weymann K, Negrotto D et al (1994) A central role of salicylic acid in plant disease resistance. Science 266:1247–1250. https://doi.org/10.1126/science.266.5188.1247

Dhar N, Short DPG, Mamo BE, Corrion AJ, Wai CM, Anchieta A et al (2019) *Arabidopsis* defense mutant *ndr1-1* displays accelerated development and early flowering mediated by the hormone gibberellic acid. Plant Sci 285:200–213. https://doi.org/10.1016/j.plantsci.2019.04.006

Dobbelaere S, Croonenborghs A, Thys A et al (1999) Phytostimulatory effect of *Azospirillum brasilense* wild type and mutant strains altered in IAA production on wheat. Plant Soil 212:153–162

Dodd IC, Zinovkina NY, Safronova VI, Belimov AA (2010) Rhizobacterial mediation of plant hormone status. Ann Appl Biol 157(3):361–379. https://doi.org/10.1111/j.1744-7348.2010.00439.x

Duca D, Lorv J, Patten CL, Rose D, Glick BR (2014) Indole-3-acetic acid in plant-microbe interactions. Antonie Van Leeuwenhoek Int J Gen Mol Microbiol. https://doi.org/10.1007/s10482-013-0095-y

Fradin EF, Zhang Z, Ayala JCJ, Castroverde CDM, Nazar RN, Robb J et al (2009) Genetic dissection of *Verticillium* wilt resistance mediated by tomato *Ve1*. Plant Physiol 150:320–332. https://doi.org/10.1111/j.1364-3703.2006.00323.x

Freiberg C, Fellay R, Bairoch A, Broughton WJ, Rosenthal A, Perret X (1997) Molecular basis of symbiosis between *Rhizobium* and legumes. Nature. https://doi.org/10.1038/387394a0

Galland M, Gamet L, Varoquaux F, Touraine B, Touraine B, Desbrosses G (2012) The ethylene pathway contributes to root hair elongation induced by the beneficial bacteria *Phyllobacterium brassicacearum* STM196. Plant Sci 190:74–81. https://doi.org/10.1016/j.plantsci.2012.03.008

Gao W, Long L, Zhu LF, Xu L, Gao WH, Sun LQ et al (2013a) Proteomic and virus-induced gene silencing (VIGS) analyses reveal that gossypol, brassinosteroids, and jasmonic acid contribute to the resistance of cotton to *Verticillium dahliae*. Mol Cell Proteomics 12:3690–3703. https://doi.org/10.1074/mcp.M113.031013

Gao X, Li F, Li M, Kianinejad AS, Dever JK, Wheeler TA et al (2013b) Cotton *GhBAK1* mediates *Verticillium* wilt resistance and cell death. J Integr Plant Biol 55:586–596. https://doi.org/10.1111/jipb.12064

Gao W, Long L, Xu L, Lindsey K, Zhang X, Zhu L (2016) Suppression of the homeobox gene *HDTF1* enhances resistance to *Verticillium dahliae* and *Botrytis cinerea* in cotton. J Integr Plant Biol 58:503–513. https://doi.org/10.1111/jipb.12432

Ghosh D, Sen S, Mohapatra S (2017) Modulation of proline metabolic gene expression in *Arabidopsis thaliana* under water-stressed conditions by a drought-mitigating *Pseudomonas putida* strain. Ann Microbiol. https://doi.org/10.1007/s13213-017-1294-y

Ghosh D, Gupta A, Mohapatra S (2019) A comparative analysis of exopolysaccharide and phytohormone secretions by four drought-tolerant rhizobacterial strains and their impact on osmotic-stress mitigation in *Arabidopsis thaliana*. World J Microbiol Biotechnol. https://doi.org/10.1007/s11274-019-2659-0

Glass NL, Kosuge T (1986) Cloning of the gene for indoleacetic acid-lysine synthetase from *Pseudomonas syringae* subsp. savastanoi. J Bacteriol. https://doi.org/10.1128/jb.166.2.598-603.1986

Glazebrook J (2005) Contrasting mechanisms of defense against biotrophic and necrotrophic pathogens. Annu Rev Phytopathol 43:220–227. https://doi.org/10.1146/annurev.phyto.43.040204.135923

Goicoechea N, Aguirreolea J, Cenoz S, Garcia-Mina JM (2000) *Verticillium dahliae* modifies the concentration of proline, soluble sugars, starch, soluble protein and abscisic acid in pepper plants. Eur J Plant Pathol 106:19–25. https://doi.org/10.1023/A:1008724816041

Gong Q, Yang Z, Wang X, Butt HI, Chen E, He S et al (2017) Salicylic acid-related cotton (*Gossypium arboreum*) ribosomal protein GaRPL18 contributes to resistance to *Verticillium dahliae*. BMC Plant Biol 3:17–59. https://doi.org/10.1186/s12870-017-1007-5

Gouda S, Kerry RG, Das G, Paramithiotis S, Shin H-S, Patra JK (2018) Revitalization of plant growth promoting rhizobacteria for sustainable development in agriculture. Microbiol Res 206:131–140. https://doi.org/10.1016/J.MICRES.2017.08.016

Guo W, Jin L, Miao Y, He X, Hu Q, Guo K et al (2016) An ethylene response-related factor, *GbERF1-like*, from *Gossypium barbadense* improves resistance to *Verticillium dahliae* via activating lignin synthesis. Plant Mol Biol 91:305–318. https://doi.org/10.1007/s11103-016-0467-6

Gupta S, Schillaci M, Walker R, Smith PMC, Watt M, Roessner U (2021) Alleviation of salinity stress in plants by endophytic plant-fungal symbiosis: current knowledge, perspectives and future directions. Plant Soil 461(1–2):219–244. https://doi.org/10.1007/S11104-020-04618-W

He X, Zhu L, Xu L, Guo W, Zhang X (2016) *GhATAF1*, a NAC transcription factor, confers abiotic and biotic stress responses by regulating phytohormonal signaling networks. Plant Cell Rep 35:2167–2179. https://doi.org/10.1007/s00299-016-2027-6

He X, Wang T, Zhu W, Wang Y, Zhu L (2018a) *GhHB12*, a HD-ZIP I transcription factor, negatively regulates the cotton resistance to *Verticillium dahliae*. Int J Mol Sci 19:3997. https://doi.org/10.3390/ijms19123997

He X, Zhu L, Wassan GM, Wang Y, Miao Y et al (2018b) *GhJAZ2* attenuates cotton resistance to biotic stresses via the inhibition of the transcriptional activity of *GhbHLH171*. Mol Plant Pathol 19:896–908. https://doi.org/10.1111/mpp.12575

Hou X, Lee LYC, Xia K, Yan Y, Yu H (2010) DELLAs modulate jasmonate signaling via competitive binding to JAZs. Dev Cell 19:884–894. https://doi.org/10.1016/j.devcel.2010.10.024

Hu Q, Min L, Yang X, Jin S, Zhang L, Li Y, Ma Y, Qi X, Li D, Liu H, Lindsey K, Zhu L, Zhang X (2018) Laccase GhLac1 modulates broad-spectrum biotic stress tolerance via manipulating phenylpropanoid pathway and jasmonic acid synthesis. Plant Physiol 176:1808–1823. https://doi.org/10.1104/pp.17.01628

Hu X, Puri KD, Gurung S, Klosterman SJ, Wallis CM, Britton M, Durbin-Johnson B, Phinney B, Salemi M, Short DPG, Subbarao KV (2019) Proteome and metabolome analyses reveal differential responses in tomato-*Verticillium dahliae*-interactions. J Proteom 207:103449. https://doi.org/10.1016/j.jprot.2019.103449

Iqbal A, Hasnain S (2013) Aeromonas punctata PNS-1: A promising candidate to change the root morphogenesis of *Arabidopsis thaliana* in MS and sand system. Acta Physiol Plant 35(3):657–665. https://doi.org/10.1007/S11738-012-1106-8

Jia ZQ, Yuan HY, Li YZ (2007) NO and H_2O_2 induced by *Verticillium dahliae* toxins and its influence on the expression of *GST* gene in cotton suspension cells. Chin Sci Bull 52:1347–1354. https://doi.org/10.1007/s11434-007-0211-3

Johansson A, Staal J, Dixelius C (2006) Early responses in the *Arabidopsis*-*Verticillium longisporum* pathosystem are dependent on NDR1, JA- and ET-associated signals via cytosolic NPR1 and RFO1. Mol Plant Microbe Interact 19:958–969. https://doi.org/10.1094/MPMI-19-0958

Kamble A, Koopmann B, von Tiedemann A (2013) Induced resistance to *Verticillium longisporum* in *Brassica napus* by b-aminobutyric acid. Plant Pathol 62:552–561. https://doi.org/10.1111/j.1365-3059.2012.02669.x

Kang S-M, Khan AL, Waqas M, You Y-H, Kim J-H, Kim J-G, Hamayun M, Lee I-J (2014a) Plant growth-promoting rhizobacteria reduce adverse effects of salinity and osmotic stress by regulating phytohormones and antioxidants in *Cucumis sativus*. J Plant Interact 9(1):673–682. https://doi.org/10.1080/17429145.2014.894587

Kang S-M, Latif Khan A, You Y-H, Kim J-G, Kamran M, Lee I-J (2014b) Gibberellin production by newly isolated strain *Leifsonia soli* SE134 and its potential to promote plant growth. J Microbiol Biotechnol 24(1):106–112. https://doi.org/10.4014/jmb.1304.04015

Kang S-M, Radhakrishnan R, Khan AL, Kim M-J, Park J-M, Kim B-R, Shin D-H, Lee I-J (2014c) Gibberellin secreting rhizobacterium, *Pseudomonas putida* H-2-3 modulates the hormonal and stress physiology of soybean to improve the plant growth under saline and drought conditions. Plant Physiol Biochem 84:115–124. https://doi.org/10.1016/j.plaphy.2014.09.001

Khan AL, Halo BA, Elyassi A, Ali S, Al-Hosni K, Hussain J, Al-Harrasi A, Lee I-J (2016) Indole acetic acid and ACC deaminase from endophytic bacteria improves the growth of *Solanum lycopersicum*. Electron J Biotechnol 21:58–64. https://doi.org/10.1016/J.EJBT.2016.02.001

Kochar M, Upadhyay A, Srivastava S (2011) Indole-3-acetic acid biosynthesis in the biocontrol strain *Pseudomonas fluorescens* Psd and plant growth regulation by hormone overexpression. Res Microbiol. https://doi.org/10.1016/j.resmic.2011.03.006

Koga J, Adachi T, Hidaka H (1991) Molecular cloning of the gene for indolepyruvate decarboxylase from *Enterobacter cloacae*. MGG Mol Gen Genet. https://doi.org/10.1007/BF00273581

Krishna P (2003) Brassinosteroid-mediated stress responses. J Plant Growth Regul 22:289–297. https://doi.org/10.1007/s00344-003-0058-z

Kudoyarova GR, Vysotskaya LB, Arkhipova TN, Kuzmina LY, Galimsyanova NF, Sidorova LV, Gabbasova IM, Melentiev AI, Veselov SY (2017) Effect of auxin producing and phosphate solubilizing bacteria on mobility of soil phosphorus, growth rate, and P acquisition by wheat plants. Acta Physiol Plant 39(11). https://doi.org/10.1007/s11738-017-2556-9

Kudoyarova G, Arkhipova T, Korshunova T, Bakaeva M, Loginov O, Dodd IC (2019) Phytohormone mediation of interactions between plants and non-symbiotic growth promoting bacteria under edaphic stresses. Front Plant Sci 10. https://doi.org/10.3389/fpls.2019.01368

Kumla J, Suwannarach N, Matsui K, Lumyong S (2020) Biosynthetic pathway of indole-3-acetic acid in ectomycorrhizal fungi collected from northern Thailand. PLoS One. https://doi.org/10.1371/journal.pone.0227478

Lee K-E, Radhakrishnan R, Kang S-M, You Y-H, Joo G-J, Lee I-J, Ko J-H, Kim J-H (2015) *Enterococcus faecium* LKE12 cell-free extract accelerates host plant growth via gibberellin and indole-3-acetic acid secretion. J Microbiol Biotechnol 25(9):1467–1475. https://doi.org/10.4014/jmb.1502.02011

Li C, He X, Luo X, Xu L, Liu L, Min L et al (2014) Cotton *WRKY1* mediates the plant defense-to-development transition during infection of cotton by *Verticillium dahliae* by activating *JASMONATE ZIM-DOMAIN1* expression. Plant Physiol 166:2179–2194. https://doi.org/10.1104/pp.114.246694

Li N, Wang W, Bitas V, Subbarao K, Liu X, Kang S (2018) Volatile compounds emitted by diverse *Verticillium* species enhance plant growth by manipulating auxin signaling. Mol Plant Microbe Interact 31:102–1031. https://doi.org/10.1094/MPMI-11-17-0263-R

Li J, Zingen-Sell I, Buchenauer H (1996) Induction of resistance of cotton plants to *Verticillium* wilt and of tomato plants to *Fusarium* wilt by 3-aminobutyric acid and methyl jasmonate. J Plant Dis Protect 103(3):288–299. https://www.jstor.org/stable/43216097

Liao D, Wang S, Cui M, Liu J, Chen A, Xu G (2018) Phytohormones regulate the development of arbuscular mycorrhizal symbiosis. Int J Mol Sci. https://doi.org/10.3390/ijms19103146

Liebrand TWH, van den Berg GCM, Zhang Z, Smit P, Cordewener JHG, America AHP et al (2013) Receptor-like kinase *SOBIR1/EVR* interacts with receptor-like proteins in plant immunity against fungal infection. Proc Natl Acad Sci USA 110:10010–10015. https://doi.org/10.1073/pnas.1220015110

Liu F, Xing S, Ma H, Du Z, Ma B (2013) Cytokinin-producing, plant growth-promoting rhizobacteria that confer resistance to drought stress in *Platycladus orientalis* container seedlings. Appl Microbiol Biotechnol 97(20):9155–9164. https://doi.org/10.1007/s00253-013-5193-2

Liu T, Song T, Zhang X, Yuan H, Su L, Li W et al (2014) Unconventionally secreted effectors of two filamentous pathogens target plant salicylate biosynthesis. Nat Commun 5:4686. https://doi.org/10.1038/ncomms5686

MacDonald E, Powell G, Regier D, Glass NL, Roberto F, Kosuge T, Morris R (1986) Secretion of zeatin, ribosylzeatin, and ribosyl-1″-methylzeatin by *Pseudomonas savastanoi*: plasmid-coded cytokinin biosynthesis. Plant Physiology (bethesda). https://doi.org/10.1104/pp.82.3.742

Mansoori B, Smith CJ (2005) Elicitation of ethylene by *Verticillium albo-atrum* phytotoxins in potato. J Phytopathol 153:143–149. https://doi.org/10.1111/j.1439-0434.2005.00943.x

Mantelin S, Touraine B (2003) Plant growth-promoting bacteria and nitrate availability: impacts on root development and nitrate uptake. J Exp Bot 55(394):27–34. https://doi.org/10.1093/jxb/erh010

Marulanda A, Barea J-M, Azcón R (2009) Stimulation of plant growth and drought tolerance by native microorganisms (AM fungi and bacteria) from dry environments: mechanisms related to bacterial effectiveness. J Plant Growth Regul 28(2):115–124. https://doi.org/10.1007/s00344-009-9079-6

Misaghi I, Kosuge T, Devay JE (1972) Changes in cytokinin activity associated with development of *Verticillium* wilt and water stress in cotton plants. Physiol Plant Pathol 2:187–196. https://doi.org/10.1016/0048-4059(72)90001-X

Numan M, Bashir S, Khan Y, Mumtaz R, Shinwari ZK, Khan AL, Khan A, AL-Harrasi A (2018) Plant growth promoting bacteria as an alternative strategy for salt tolerance in plants: a review. Microbiol Res 209:21–32. https://doi.org/10.1016/J.MICRES.2018.02.003

Ortiz-Castro R, Díaz-Pérez C, Martínez-Trujillo M, del Río RE, Campos-García J, López-Bucio J (2011) Transkingdom signaling based on bacterial cyclodipeptides with auxin activity in plants. Natl Acad Sci 108.https://doi.org/10.1073/pnas.1006740108

Pantelides IS, Tjamos SE, Paplomatas EJ (2010a) Insights into the role of ethylene perception in tomato resistance to vascular infection by *Verticillium dahliae*. Plant Path 59:130–138. https://doi.org/10.1111/j.1365-3059.2009.02206.x

Pantelides IS, Tjamos SE, Paplomatas E. J. (2010b). Ethylene perception via *ETR1* is required in *Arabidopsis* infection by *Verticillium dahliae*. Mol Plant Pathol 11:191–202. https://doi.org/10.1111/j.1364-3703.2009.00592.x

Patrick TW, Hall R, Fletcher RA (1977) Cytokinin levels in healthy and *Verticillium*-infected tomato plants. Can J Bot 55:377–382. https://doi.org/10.1139/b77-048

Patten CL, Glick BR (2002b) Role of *Pseudomonas putida* indoleacetic acid in development of the host plant root system. Appl Environ Microbiol. https://doi.org/10.1128/AEM.68.8.3795-3801.2002b

Patten CL, Blakney AJC, Coulson TJD (2013) Activity distribution and function of indole-3-acetic acid biosynthetic pathways in bacteria. Crit Rev Microbiol.https://doi.org/10.3109/1040841X.2012.716819

Patten CL, Glick BR (2002a) Regulation of indoleacetic acid production in *Pseudomonas putida* GR12-2 by tryptophan and the stationary-phase sigma factor RpoS. Can J Microbiol. https://doi.org/10.1139/w02-053

Pegg GF (1976) The response of ethylene-treated tomato plants to infection by *Verticillium albo-atrum*. Physiol Plant Path 9:215–226. https://doi.org/10.1016/0048-4059(76)90055-2

Pegg GF, Brady BL (2002) *Verticillium* wilts. CABI Publishing, New York

Pegg GF, Cronshaw DK (1976) Ethylene production in tomato plants infected with *Verticillium albo-atrum*. Physiol Plant Path 8:279–295. https://doi.org/10.1016/0048-4059(76)90022-9

Pereyra MA, García P, Colabelli MN, Barassi CA, Creus CM (2012) A better water status in wheat seedlings induced by *Azospirillum* under osmotic stress is related to morphological changes in xylem vessels of the coleoptile. Appl Soil Ecol 53:94–97. https://doi.org/10.1016/J.APSOIL.2011.11.007

Pons S, Fournier S, Chervin C, Bécard G, Rochange S, Dit Frey NF, Pagès VP (2020) Phytohormone production by the arbuscular mycorrhizal fungus *Rhizophagus irregularis*. PLoS One.https://doi.org/10.1371/journal.pone.0240886

Poupin MJ, Timmermann T, Vega A, Zuñiga A, González B (2013) Effects of the plant growth-promoting bacterium *Burkholderia phytofirmans* PsJN throughout the life cycle of *Arabidopsis thaliana*. PLoS One 8(7). https://doi.org/10.1371/journal.pone.0069435

Poupin MJ, Greve M, Carmona V, Pinedo I (2016) A complex molecular interplay of auxin and ethylene signaling pathways is involved in Arabidopsis growth promotion by *Burkholderia phytofirmans* PsJN. Front Plant Sci 7(APR2016). https://doi.org/10.3389/FPLS.2016.00492/FULL

Qin J, Wang K, Sun L, Xing H, Wang S, Li L et al (2018) The plant-specific transcription factors CBP60g and SARD1 are targeted by a *Verticillium* secretory protein VdSCP41 to modulate immunity. eLife 7:e34902. https://doi.org/10.7554/eLife.34902

Raza FFA, Faisal M (2013) Growth promotion of maize by desiccation tolerant *Micrococcus luteus*-chp37 isolated from Cholistan desert, Pakistan. AJCS 7(Issue 11)

Reusche M, Klaskova J, Thole K, Truskina J, Novak O, Janz D et al (2013) Stabilization of cytokinin levels enhances *Arabidopsis* resistance against *Verticillium longisporum*. Mol Plant Microbe Interact 26:850–860. https://doi.org/10.1094/MPMI-12-12-0287-R

Robison MM, Griffith M, Pauls KP, Glick BR (2001a) Dual role for ethylene in susceptibility of tomato to *Verticillium* wilt. J Phytopath 149:385–388. https://doi.org/10.1111/j.1439-0434.2001.tb03867.x

Robison MM, Shah S, Tamot B, Pauls KP, Moffatt BA, Glick BR (2001b) Reduced symptoms of *Verticillium* wilt in transgenic tomato expressing a bacterial ACC deaminase. Mol Plant Path 2:135–145. https://doi.org/10.1046/j.1364-3703.2001.00060.x

Roos J, Bejai S, Oide S, Dixelius C (2014) *RabGAP22* is required for defense to the vascular pathogen *Verticillium longisporum* and contributes to stomata immunity. PLoS One 4, 9(2):e88187. https://doi.org/10.1371/journal.pone.0088187

Ryu CM, Faragt MA, Hu CH, Reddy MS, Wei HX, Paré PW, Kloepper JW (2003) Bacterial volatiles promote growth in *Arabidopsis*. Proc Natl Acad Sci USA. https://doi.org/10.1073/pnas.0730845100

Saharan BS, Nehra V (2011) Plant growth promoting rhizobacteria: a critical review. Life Sci Med Res 2011

Sakakibara H (2006) Cytokinins: activity, biosynthesis, and translocation. Annu Rev Plant Biol. https://doi.org/10.1146/annurev.arplant.57.032905.105231

Salomon MV, Bottini R, de Souza Filho GA, Cohen AC, Moreno D, Gil M, Piccoli P (2014) Bacteria isolated from roots and rhizosphere of *Vitis vinifera* retard water losses, induce abscisic acid accumulation and synthesis of defense-related terpenes in in vitro cultured grapevine. Physiol Plant 151(4):359–374. https://doi.org/10.1111/ppl.12117

Sandhya V, Ali SZ, Venkateswarlu B, Reddy G, Grover M (2010) Effect of osmotic stress on plant growth promoting *Pseudomonas* spp. Arch Microbiol 192(10):867–876. https://doi.org/10.1007/s00203-010-0613-5

Sandhya V, Ali SKZ, Grover M, Reddy G, Venkateswarlu B (2009) Alleviation of drought stress effects in sunflower seedlings by the exopolysaccharides producing *Pseudomonas putida* strain GAP-P45. Biol Fertil Soils 46(1):17–26. https://doi.org/10.1007/s00374-009-0401-z

Sawada K (1912) Diseases of agricultural products in Japan. Form Agric Rev 63:10–16

Scholz SS, Schmidt-Heck W, Guthke R, Furch ACU, Reichelt M, Gershenzon J et al (2018) *Verticillium* d*ahliae-Arabidopsis* interaction causes changes in gene expression profiles and jasmonate levels on different time scales. Front Microbiol 9:217. https://doi.org/10.3389/fmicb.2018.00217

Selvakumar G, Bindu GH, Bhatt RM, Upreti KK, Paul AM, Asha A, Shweta K, Sharma M (2018) Osmotolerant cytokinin producing microbes enhance tomato growth in deficit irrigation conditions. Proc Natl Acad Sci India Sect B Biol Sci 88(2):459–465. https://doi.org/10.1007/s40011-016-0766-3

Shah DA, Sen S, Shalini A, Ghosh D, Grover M, Mohapatra S (2016) An auxin secreting *Pseudomonas putida* rhizobacterial strain that negatively impacts water-stress tolerance in *Arabidopsis thaliana*. Rhizosphere 3(P1). https://doi.org/10.1016/j.rhisph.2016.11.002

Shao J, Li S, Zhang N, Cui X, Zhou X, Zhang G, Shen Q, Zhang R (2015) Analysis and cloning of the synthetic pathway of the phytohormone indole-3-acetic acid in the plant-beneficial *Bacillus amyloliquefaciens* SQR9. Microb Cell Factories. https://doi.org/10.1186/s12934-015-0323-4

Shi FM, Li YZ (2008) *Verticillium dahliae* toxins-induced nitric oxide production in *Arabidopsis* is major dependent on nitrate reductase. BMB Rep 41:79–85. https://doi.org/10.5483/bmbrep.2008.41.1.079

Shi FM, Yao LL, Pei BL, Zhou Q, Li XL, Li Y et al (2009) Cortical microtubule as a sensor and target of nitric oxide signal during the defense responses to *Verticillium dahliae* toxins in *Arabidopsis*. Plant Cell Environ 32:428–438. https://doi.org/10.1111/j.1365-3040.2009.01939.x

Shi CL, Park HB, Lee JS, Ryu S, Ryu CM (2010) Inhibition of primary roots and stimulation of lateral root development in *Arabidopsis thaliana* by the rhizobacterium *Serratia marcescens* 90-166 is through both auxin-dependent and -independent signaling pathways. Mol Cells 29(3):251–258. https://doi.org/10.1007/s10059-010-0032-0

Spaepen S, Vanderleyden J (2011) Auxin and plant-microbe interactions. Cold Spring Harb Perspect Biol 3(4). https://doi.org/10.1101/cshperspect.a001438

Studt L, Schmidt FJ, Jahn L, Sieber CMK, Connolly LR, Niehaus E-M et al (2013) Two histone deacetylases, FfHda1 and FfHda2, are important for *Fusarium fujikuroi* secondary metabolism and virulence. Appl Environ Microbiol 79:7719–7734. https://doi.org/10.1128/AEM.01557-13

Su F, Gilard F, Guérard F, Citerne S, Clément C, Vaillant-Gaveau N, Dhondt-Cordelier S (2016) Spatio-temporal responses of *Arabidopsis* leaves in photosynthetic performance and metabolite contents to *Burkholderia phytofirmans* PsJN. Front Plant Sci 7(MAR2016). https://doi.org/10.3389/FPLS.2016.00403/FULL

Taiz L, Zeiger E, Møller IM, Murphy A (2015) Plant physiology and development, 6th edn. In: Sinauer Associates (vol 1)

Takeda N, Handa Y, Tsuzuki S, Kojima M, Sakakibara H, Kawaguchi M (2015) Gibberellins interfere with symbiosis signaling and gene expression and alter colonization by Arbuscular Mycorrhizal fungi in *Lotus Japonicus*. Plant Physiol. https://doi.org/10.1104/pp.114.247700

Takei K, Sakakibara H, Sugiyama T (2001) Identification of genes encoding adenylate Isopentenyl-transferase, a cytokinin biosynthesis enzyme, in *Arabidopsis thaliana*. J Biol Chem. https://doi.org/10.1074/jbc.M102130200

Tjamos SE, Flemetakis E, Paplomatas EJ, Katinakis P (2005) Induction of resistance to *Verticillium dahliae* in *Arabidopsis thaliana* by the biocontrol agent K-165 and pathogenesis-related proteins gene expression. Mol Plant Microbe Interact 18:555–561. https://doi.org/10.1094/MPMI-18-0555

Tsukanova KA, Chebotar V, Meyer JJM, Bibikova TN (2017) Effect of plant growth-promoting Rhizobacteria on plant hormone homeostasis. S Afr J Bot 113:91–102. https://doi.org/10.1016/J.SAJB.2017.07.007

Tully RE, Van Berkum P, Lovins KW, Keister DL (1998) Identification and sequencing of a cytochrome P450 gene cluster from *Bradyrhizobium japonicum*. Biochim Biophys Acta Gene Struct Expr. https://doi.org/10.1016/S0167-4781(98)00069-4

Ul Hassan T, Bano A (2019) Construction of IAA-Deficient Mutants of Pseudomonas moraviensis and their comparative effects with wild type strains as bio-inoculant on wheat in saline sodic soil. Geomicrobiol J 36(4). https://doi.org/10.1080/01490451.2018.1562498

Vacheron J, Desbrosses G, Bouffaud M-L, Touraine B, Moënne-Loccoz Y, Muller D, Legendre L, Wisniewski-Dyé F, Prigent-Combaret C (2013) Plant growth-promoting rhizobacteria and root system functioning. Front Plant Sci 4:356. https://doi.org/10.3389/fpls.2013.00356

Vejan P, Abdullah R, Khadiran T, Ismail S, Nasrulhaq Boyce A (2016) Role of plant growth promoting rhizobacteria in agricultural sustainability—a review. Molecules 21(5):573. https://doi.org/10.3390/molecules21050573

Wang JY, Cai Y, Gou JY, Mao YB, Xu YH, Jiang WH et al (2004) *Vd*NEP, an elicitor from *Verticillium dahliae*, induces cotton plant wilting. Appl Environ Microbiol 70:4989–4995. https://doi.org/10.1128/AEM.70.8.4989-4995.2004

Wang Z-Y, Bai M-Y, Oh E, Zhu J-Y (2012) Brassinosteroid signaling network and regulation of photomorphogenesis. Ann Rev Genet 46:701–724. https://doi.org/10.1146/annurev-genet-102209-163450

Wang J, Zhang Y, Li Y, Wang X, Nan W, Hu Y, Zhang H, Zhao C, Wang F, Li P, Shi H, Bi Y (2015) Endophytic microbes *Bacillus* sp. LZR216-regulated root development is dependent on polar auxin transport in *Arabidopsis* seedlings. Plant Cell Rep 34(6):1075–1087. https://doi.org/10.1007/S00299-015-1766-0

Waqas M, Khan A, Kamran M, Hamayun M, Kang S (2012) Endophytic fungi produce gibberellins and indoleacetic acid and promotes host-plant growth during stress. Molecules 17:10754–10773. https://doi.org/10.3390/molecules170910754

Xie H, Pasternak JJ, Glick BR (1996) Isolation and characterization of mutants of the plant growth-promoting rhizobacterium *Pseudomonas putida* GR12-2 that overproduce indoleacetic acid. Curr Microbiol. https://doi.org/10.1007/s002849900012

Xie DX, Feys BF, James S, Nieto-Rostro M, Turner JG (1998) COI1: an *Arabidopsis* gene required for jasmonate-regulated defense and fertility. Science 280:1091–1094. https://doi.org/10.1126/science.280.5366.1091

Xie B, Xu K, Hong XZ, San FC (2005) Isolation of transposon mutants from *Azospirillum brasilense* Yu62 and characterization of genes involved in indole-3-acetic acid biosynthesis. FEMS Microbiol Lett. https://doi.org/10.1016/j.femsle.2005.05.020

Yang S, Zhang Q, Guo J, Charkowski AO, Glick BR, Ibekwe AM, Cooksey DA, Yang CH (2007) Global effect of indole-3-acetic acid biosynthesis on multiple virulence factors of *Erwinia chrysanthemi* 3937. Appl Environ Microbiol. https://doi.org/10.1128/AEM.01770-06

Yang CL, Liang S, Wang HY, Han LB, Wang FX, Cheng HQ et al (2015) Cotton major latex protein 28 functions as a positive regulator of the *ethylene responsive factor 6* in defense against *Verticillium dahliae*. Mol Plant 8:399–411. https://doi.org/10.1016/j.molp.2014.11.023

Yang J, Ma Q, Zhang Y, Wang X, Zhang G, Ma Z (2016) Molecular cloning and functional analysis of *GbRVd*, a gene in *Gossypium barbadense* that plays an important role in conferring resistance to Verticillium wilt. Gene 575:687–694. https://doi.org/10.1016/j.gene.2015.09.046

Yao LL, Pei BL, Zhou Q, Li YZ (2012) NO serves as a signaling intermediate downstream of H_2O_2 to modulate dynamic microtubule cytoskeleton during responses to VD-toxins in *Arabidopsis*. Plant Signal Behav 7:174–177. https://doi.org/10.4161/psb.18768

Zhang H, Kim MS, Krishnamachari V, Payton P, Sun Y, Grimson M, Farag MA, Ryu CM, Allen R, Melo IS, Paré PW (2007) Rhizobacterial volatile emissions regulate auxin homeostasis and cell expansion in *Arabidopsis*. Planta 226(4):839–851. https://doi.org/10.1007/S00425-007-0530-2

Zheng X, Koopmann B, von Tiedemann A (2019) Role of salicylic acid and components of the phenylpropanoid pathway in basal and cultivar-related resistance of oilseed rape (*Brassica napus*) to *Verticillium longisporum*. Plants 8(11):491. https://doi.org/10.3390/plants8110491

Zhou BJ, Jia PS, Gao F, Guo HS (2012) Molecular characterization and functional analysis of a necrosis- and ethylene-inducing, protein-encoding gene family from *V. dahliae*. Mol Plant Microbe Interact 25:964–975. https://doi.org/10.1094/MPMI-12-11-0319

Zhou Y, Sun L, Wassan GM, He X, Shaban M, Zhang L et al (2019) *GbSOBIR1* confers *Verticillium* wilt resistance by phosphorylating the transcriptional factor *GbbHLH171* in *Gossypium barbadense*. Plant Biotechnol J 17:152–163. https://doi.org/10.1111/pbi.12954

Zhu S, Gao F, Cao X, Chen M, Ye G, Wei C et al (2005) The rice dwarf virus P2 protein interacts with ent-kaurene oxidases in vivo, leading to reduced biosynthesis of gibberellins and rice dwarf symptoms. Plant Physiol 139:1935–1945. https://doi.org/10.1104/pp.105.072306

Zupan JR, Zambryski P (1995) Transfer of T-DNA from agrobacterium to the plant cell. Plant Physiol.https://doi.org/10.1104/pp.107.4.1041