We are IntechOpen, the world's leading publisher of Open Access books Built by scientists, for scientists

5,800
Open access books available

142,000
International authors and editors

180M
Downloads

Our authors are among the

154
Countries delivered to

TOP 1%
most cited scientists

12.2%
Contributors from top 500 universities

BOOK CITATION INDEX
CLARIVATE ANALYTICS
INDEXED

WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Auxins-Interkingdom Signaling Molecules

Aqsa Tariq and Ambreen Ahmed

Abstract

Phytohormones play a fundamental role in the development of plants. Among various phytohormones produced by the plants, Auxins act as a master hormone that plays a major role during plant development and differentiation through cell division. Besides plants, many rhizospheric microorganisms are also capable of producing auxins specifically indole-3-acetic acid (IAA), that act as signaling molecules for the regulation of gene expressions in plants. However, bacterial IAA is majorly linked with the modulation of plant roots architecture and developing positive plant-microbe interactions. Bacterial auxin modifies root morphology by enhancing root length, forming adventitious root and root hair, thereby, increasing surface area for water and nutrient absorption affecting various aspects of plant biology in a number of ways. Bacteria mostly utilize tryptophan, present in plant root exudates, to synthesize IAA that eventually helps bacteria to colonize roots by establishing beneficial associations with plant roots. Auxins also stimulate the formation of exopolysaccharides and biofilms that help bacterial root colonization. Auxins have given the survival benefit to rhizobacteria that make them more competent to establish symbiotic interaction with plants. Synergistic and antagonistic interactions of auxins (both interkingdom and Intrakingdom) with other phytohormones play a key role in plant development and growth improvement.

Keywords: Auxins, bacterial IAA, phytostimulation, Indole-3-acetamide, Tryptophan

1. Introduction

Auxins are mainly synthesized in meristematic tissues and transported to other plant parts. Auxins play a critical role in controlling various processes during growth and development across variable environmental conditions, even at lower concentrations, these can modulate gene expression by interacting with specific proteins involved in the transcription process [1]. The plant rhizosphere is enriched with a diversity of microflora that directly contributes to their growth. The rhizosphere microbiota has the ability to produce phytohormones as a signaling molecule for inter and intraspecies communications. The synthesis and release of auxins establish a mutualistic or morbific link between organisms. Indole-3-acetic acid (IAA) is a widely produced rhizobacterial signaling phytohormone. Primarily, auxin controls various physiological processes, such as cell division, elongation, phototactic, and geotactic responses, in plants [2]. Thus, in nature, plants are receiving endogenous and exogenous signals simultaneously influencing their developmental patterns. Endogenous auxin can either be free (active auxin) or act as storage intermediates

as conjugated compounds with amino acids and sugars [3]. Since higher auxin levels cause inhibitory effects, therefore, homeostasis and coordination of auxin signaling within plants and their surroundings are necessary for their regular growth and development. Endogenous auxin levels suggest the type of interactions between plant and rhizobacteria. Generally, three possible plant-bacterial IAA associations have been stated so far, first, due to direct transfer of bacterial IAA genes into host cell; second, due to bacteria living and releasing IAA within plant tissues and lastly, due to bacteria colonizing plant surfaces and producing IAA [4]. The first two associations usually result from pathogenic interactions. The knowledge of deciphering these signals and their outcomes is critical for the development of strategies for sustainable agricultural practices. Thus, the present chapter highlights the significant role of bacterial IAA as a potent microbial signaling molecule regarding beneficial plant-rhizobacterial interactions which are important for ecological resilience and sustainability.

2. Biosynthetic pathways of auxins

Conferring to key intermediate compounds, five different pathways for IAA synthesis have been reported in bacteria using tryptophan precursors [5]. Rhizobacteria use tryptophane either from plant root exudates or synthesize through chorismate precursor using trp gene by shikimate pathway [6, 7]. Rhizobia are an example of rhizobacteria that utilize host tryptophan for IAA synthesis [8]. Zhang *et al*. [9] analyzed 7282 prokaryotic genomes and revealed that 82.2% were efficient IAA producers from tryptophan precursors. However, Brown and Burlingham [10] observed a low amount of auxin in bacterial cultures without tryptophan indicating the fact that bacteria might have the ability to synthesize auxin without using tryptophan [11, 12]. Later, this was confirmed by the studies of Prinsen *et al*. [13] who reported the ability of IAA production by *Azospirillum brasilense* following tryptophan-independent pathway. However, there is a lack of information regarding genes, enzymes, or proteins involved. Recently, Li *et al*. [14] and Ahmad *et al*. [15] have also reported IAA biosynthesis in the absence of an exogenous tryptophan supply in Arthrobacter pascens ZZ21 and *Micrococcus aloeverae* DCB-20, respectively, however, no genetic evidence has been provided so far. Moreover, more than one auxin biosynthetic pathway functions within plants and bacteria together [9, 14].

In vitro production of IAA was observed to be highly influenced by bacterial growth conditions and the presence of tryptophan [16–18]. Higher auxin production by bacterial strains has been observed under increasing tryptophan concentrations [19]. Moreover, the genetic elements involved in the regulation of bacterial IAA have been demonstrated in *A. brasilense*. The key gene involved in this process is *ipdC* gene. Moreover, increased expression of *ipdC* gene was observed under increasing IAA levels indicating the involvement of auxin signaling in regulating its biosynthesis, a positive-feedback regulation. *In silico* analysis revealed that *RpoN* binding site is responsible for regulating the expression of *ipdC* gene [20]. Various transcriptional factors influencing *ipdC* gene expression have been identified in different bacterial species. Patten and Glick [21] described RpoS to regulate ipdC transcription in *Pseudomonas putida* and *P. agglomerans*, respectively. Similarly, *GacS/GacA* system has been identified in *Pseudomonas chlororaphis* as a negative regulator of tryptophan-dependent routes of IAA production [22]. Ryu and Patten [23] identified *TyrR* protein to regulate the induction of *ipdC* gene expression in Enterobacter cloacae in response to tryptophan. A high similarity of various auxin synthetic pathways has been observed between plants and bacteria with slightly

different intermediate products. An overview of various auxin biosynthetic pathways has been given below:

Indole-3-acetamide (IAM) pathway: It involves two steps, conversion of tryptophan to Indole-3-acetamide by tryptophan-2-monooxygenase followed by conversion to IAA by IAM hydrolase [4]. The phytopathogens, such as *Agrobacterium tumefaciens*, *Pantoea agglomerans,* and *Pseudomonas syringae,* and some plant growth-promoting rhizobacterial (PGPR) genera, such as Rhizobium and Bradyrhizobium, have exhibited this pathway [7, 24].

Indole-3-pyruvic acid (IPyA) pathway: It involves three steps, first formation of Indole-3-pyruvic acid by aminotransferase occurs followed by decarboxylation into indole-3-acetaldehyde which is finally oxidized into IAA (**Figure 1**). The key enzyme in this pathway is identified as indole-3-pyruvate decarboxylase (encoded by ipdC gene) [4]. This pathway is present in a broad range of bacterial species from phytopathogenic bacteria (*P. agglomerans*) to PGPR (*Pseudomonas*, *Azospirillum*, *Enterobacter*, *Bacillus*, *Paenibacillus*, *Bradyrhizobium*, and *Rhizobium*) and even in cyanobacteria [7, 25].

Tryptamine (TAM) pathway: It involves decarboxylation of tryptophan to tryptamine which is then converted into indole-3-acetaldehyde by amine oxidase
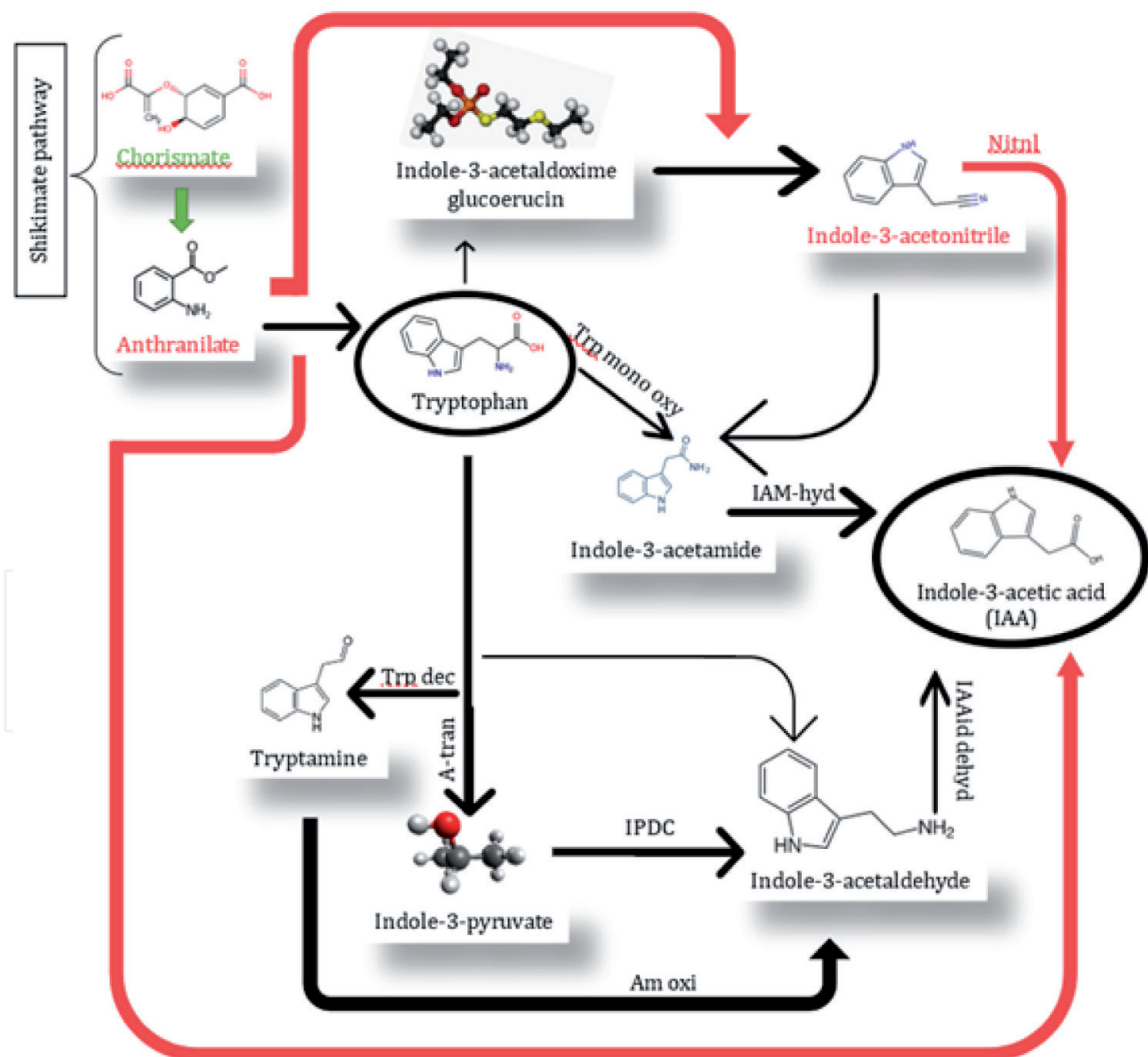
Figure 1.
Various tryptophan-dependent and -independent pathways for auxin (IAA) synthesis. Red lines indicate the tryptophan-independent pathway of IAA synthesis. Black lines show tryptophan-dependent pathways. Chorismate is the precursor of both mechanisms. [A- trans - aminotransferase; Trp dec - tryptophan decarboxylase; Am oxi - amine-oxidase; IPDC - Indole-3-pyruvate decarboxylase; IAM-hyd - Indole-3-acetamide hydrolase; Nitril - Nitrilase; IAAid dehyd – Indole-3-acetaldehyde dehydrogenase].

followed by its oxidation to IAA [4]. This has been reported in Bacillus cereus and *Azospirillum* [7, 24].

Indole-3-acetonitrile (IAN) pathway: In this pathway, tryptophan is converted into Indole-3-acetonitrile either by indolic glucosinolates or indole-3-acetaldoxime which is then further converted into IAA by nitrilase. This pathway has also been reported in *Alcaligenes faecalis*, *A. tumefaciens*, and *Rhizobium* spp. [7, 24].

Tryptophan side-chain oxidase (TSO) pathway: This is found in Pseudomonas fluorescens CHA0 and involves direct conversion of tryptophan to indole-3-acetaldehyde which then oxidizes to IAA. This mechanism is only found in bacteria and has not been studied in plants (**Figure 1**) [7, 24].

3. IAA – Signaling molecule

a. Intrakingdom Signaling

Auxins modulate the gene expression making it inter and intrakingdom communicating chemical messenger and quorum-sensing molecule. Scott *et al*. [26] observed bacterial chemotaxis toward IAA in *P. putida*. This movement is mediated by methyl-accepting proteins that receive and transmit IAA signals to flagellar machinery [26]. Hence, the movement of PGPR toward plant roots might be due to IAA present in root exudates. This IAA also acts as a nutrient pool, thereby, chemotaxis toward IAA ensures bacterial survival within the plant environment. Moreover, the fact that most of the plant-associated rhizobacteria produce IAA indicates that IAA might have some crucial role in bacterial cells other than interacting with plants [27]. From an evolutionary perspective, bacteria gain this ability for their survival and persistence within the plant environment [28]. IAA producers are more environmentally adaptive and competitive as compared to non-producers. Studies by Bianco *et al*. [29] showed that IAA confers protection to bacteria under various abiotic conditions, such as acidity, UV, salt, and heat stress. The author observed higher production of extracellular polysaccharides (EPS), lipopolysaccharides, and biofilms in IAA overproducers that improved bacterial adherence to plant surfaces which ultimately protect bacterial cells from various environmental stresses. Moreover, overproduction of trehalose in IAA producers has been observed indicating the accumulation of osmolytes within the bacterial cell to confer osmotic protection [29]. This was further confirmed by the studies of Donati *et al*. [30]. They reported a higher survival rate of IAA-treated bacteria under oxidative, desiccation, and osmotic stress and observed increased production of EPS and biofilm. Under various stress conditions, increased IAA levels were observed within bacterial cells indicating the fact that IAA plays important role in modulating gene expression of bacterial cells and making them more competitive [31]. However, the exact mechanism is still unknown and needed to be explored. IAA also acts as a signaling molecule for various metabolic processes within bacterial cells. Van Puyvelde *et al*. [32] observed the overall changes in gene expression of a mutant strain of *A. brasilense* and noted the decreased expression of 39 genes, including the genes involved in bacterial cell respiration by affecting the expression of NADH dehydrogenase. However, on the other hand, increased expression of the nitrate-reducing system involved in aerobic denitrification and ATP-binding cassette transporters and tripartite ATP-independent periplasmic (TRAP) transporters was also observed. Van Puyvelde *et al*. [32] also noted increased expression of T6SS (Type VI Secretion System) by exogenous IAA induction which is involved in the transport of various components via injection tube from a bacterial cell to

plants cell (the mechanism by which bacteria interact directly to plant signaling pathways). Moreover, IAA also enhances the expression of genes involved in the formation of effector proteins of T3SS (Type III Secretion System) required for injection of pathogenicity within plant cells [33].

  b. Interkingdom Signaling

  Signal exchange between plant and rhizospheric bacteria occurs through the release of root exudates [34]. This signaling is key for developing and determining the nature of plant-bacterial interactions (symbiotic or pathogenic). PGPR colonization is the result of these signaling activities. Besides IAA synthesis, many rhizobacterial species have the ability to degrade IAA. This IAA degrading ability has given the advantage to bacteria for rhizospheric colonization and manipulating plant physiology for their survival. However, the mechanism of how IAA degradation is beneficial for plants and bacteria is not well studied and needed to be explored. Zuniga *et al*. [35] observed that IAA degradation by *Burkholderia phytofirmans* is key for efficient rhizosphere colonization and subsequent plant growth promotion. Any mutation in IAA degrading gene (iacC) also affects the growth promotional activity of the bacteria. In addition, auxin also interferes with the developmental pathways of the host. So, it is hypothesized that rhizobacteria synthesize and secrete auxin that is taken up by plants in such quantities that alter normal plant developmental pathways [36]. The principal feature of bacterial IAA reported by researchers is to manipulate the plant root growth (**Figure 2**). It induces the formation of root hair and enhances the growth of primary and lateral roots within their optimum range. However, at higher concentrations, it causes inhibitory effects and ceases the primary root growth [37]. It is suggested that this larger root system besides helping the host plant, also benefits its associated bacterial species and a larger root system absorbs more nutrients and strengthens the bacterial survival within the plant vicinity [38]. Moreover, IAA is considered to have a parallel role in developing and maintaining plant-rhizobacterial interactions [39]. In the
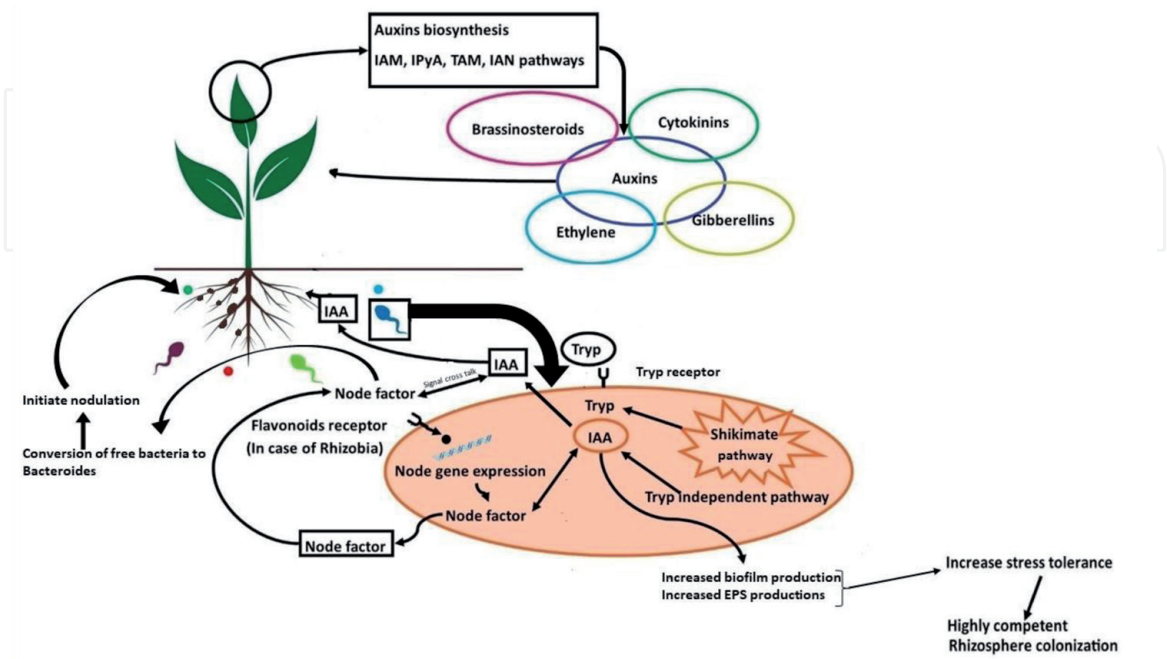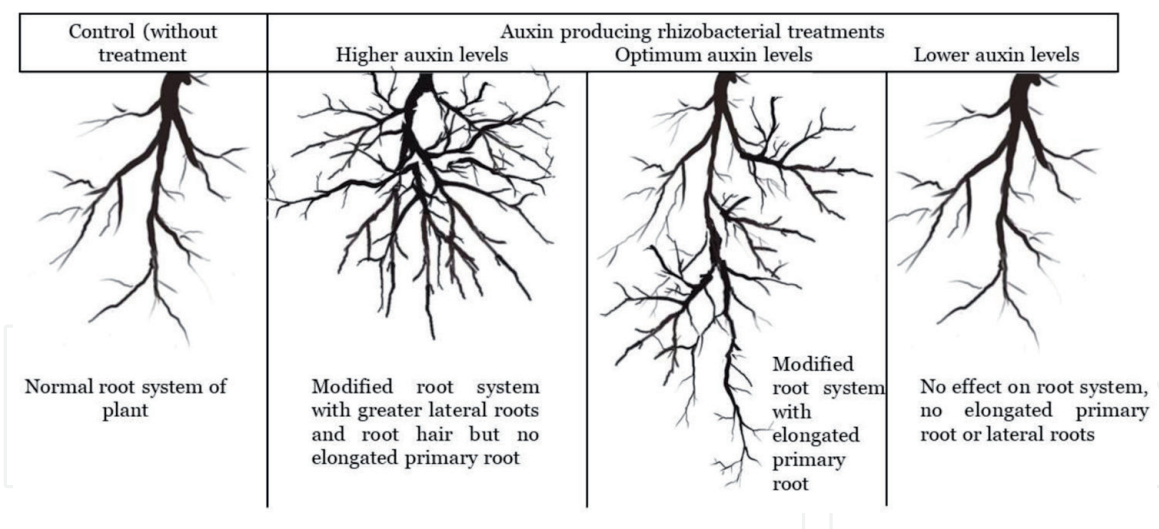

Figure 2.
Interaction of root exudates to attract various auxin-producing plant beneficial bacteria leading to various metabolic activities within bacteria and making them more competent to colonize rhizosphere. Plants also uptake bacterial auxin that interacts with other phytohormones to control overall plant development.

symbiotic association between rhizobia and legumes, the formation of macroscopic nodular structures on the roots of the host plant is considered to be formed by the action of auxin signals. Flavonoids accumulated at the sites of rhizobial entry to plant roots, inhibit auxin efflux resulting in auxin accumulation that causes excessive cell division leading to the formation of root nodules. Hence, the initiation of nodule formation is triggered by auxin signaling. Moreover, the specification of founder cells for nodule formation is also triggered by inhibition of auxin transport. Similarly, the formation of vascular bundles and the number of nodules also depend on long-distance auxin signaling. Hence, it has been hypothesized that auxin signaling triggers the formation of nodules on roots of host plants [38, 40]. Besides initiation of root nodules, IAA also modulates bacterial metabolic pathways involved in the conversion of bacteria to bacteroids for nitrogen fixation within nodules. For example, Bianco *et al*. [29] observed the activation of tricarboxylic acid and polyhydroxybutyrate cycle in *Sinorhizobium meliloti* by exogenous IAA application and in IAA-overproducer mutants (RD64). Theunis [41] observed high auxin levels in nodulated roots than in non-nodulated roots. High IAA levels also interact with nitrogen-fixing bacterial ability and enhance the nitrogen levels in nodules. In addition, the studies of Huo *et al*. [42] experimentally proven that reduction of IAA transporter genes (PIN) results in reduced nodulation. Moreover, rhizobacterial IAA also interacts with the hormonal metabolism of its associated plants. It is reported to promote the transcription of 1-aminocyclopropane-l-carboxylic acid (ACC) synthase enzyme in plants to catalyze the production of ACC deaminase enzyme which converts ACC to ammonia and α-ketobutyrate resulting in lower ethylene levels of plants. Consequently, by lowering plant ethylene levels, rhizobacteria can reduce the effect of ethylene on root growth causing plants to get nutrients and water under a wide range of stress conditions [43]. In addition, auxin signals also influence other phytohormones to regulate various plant processes. Auxin and brassinosteroids coordinate and interact to regulate the development of plant roots. Similarly, it also regulates gibberellin responses by interfering with the stability of DELLA proteins. Lower auxin levels caused reduced synthesis of gibberellins due to stabilization of DELLA proteins. Cytokinins, contrarily, have been known to suppress root formation. Therefore, overall plant growth and development depends on signaling crosstalk between auxin and other phytohormones to determine the final physiology of plants [37].

The role of bacterially produced IAA has been very significant in plant growth promotion and has been investigated by various researchers. Ahmed and Hasnain [19] studied auxin production ability and potential plant growth promotional activity of two gram-positive *Bacillus* strains and noted enhanced growth parameters, including root system and auxin content of treated plants. In another study, Fatima and Ahmed [44] investigated the role of IAA producing chromium resistant Sporosarcina saromensis and two species of Bacillus cereus on the growth of *Helianthus annuus* L. and observed an increase in plant growth parameters (shoot length, root length, fresh weight, and a number of leaves) and auxin content in treated plants. Auxin-producing bacteria stimulate seed germination and root proliferation leading to the enhanced and well-developed root system of the host plant to have greater access to water and nutrients [45]. IAA facilitates cell elongation by losing plant cell walls, thereby, increasing root length, nutrient uptake, and the release of root exudates. Enhancement in the root system of plants by exogenous application of IAA was elaborated by Vacheron *et al*. [46]. The author observed that exogenous IAA application significantly alters the root architecture of plants in a dose-dependent manner. Root growth is enhanced under optimum auxin conditions; however, higher IAA levels cease primary root growth and stimulate lateral

Figure 3.
Root growth responses to various auxin levels.

Source	Plant	Effects	Cross-signaling mechanism	Reference
Pseudomonas sp.	*Zea mays*	Root architecture modified by inhibition of primary root elongation and promotion of lateral root and root hair	Auxins interacting with volatile organic compounds	[51]
Streptomyces spp.	Soybean	Enhanced shoot growth and improved dry mass	Auxins interacting with ACC deaminase production	[52]
Bacillus sp., *Agrobacterium* sp., *Rhizobium* sp., *Phyllobacterium* sp.	*Acacia cyanophylla*	Increased shoot and root dry weight, and shoot length	Auxin + solubilized phosphate interaction	[53]
Bacillus spp.	Bamboo seedlings	Enhance chlorophyll content	Auxin trigger the chlorophyll related enzymes	[54]
Azospirillum brasilense	*Arabidopsis* sp.	Increased the expression of TARGET OF RAPAMYCIN (TOR) in shoot and root apexes and induce phosphorylation	Auxin + TOR signaling	[55]
Pseudomonas putida *Pseudomonas fluorescens*	*Arabidopsis* sp.	Increased shoot and root biomass, lateral roots number per plant, and root hair formation but no effect on primary root length	Induction of auxin signaling	[47]
Bacillus toyonensis strain Bt04	Maize roots	Enhanced root development and reduced lipid peroxidation	Induction of auxin signaling	[56]

Table 1.
Various signaling interactions of IAA.

root growth and root hair formation. In Arabidopsis sp. greater number of lateral roots have been found in the presence of high auxin-producing *Phyllobacterium brassicacearum*, however, no effect on primary root was present. Higher levels of auxins trigger lateral root formation and initiate root hair formations. However, if the auxin concentrations in plant root do not reach optimum levels even after uptake of bacterial IAA, root growth remains unaffected. Low auxin-producing *A. brasilense* has not shown any improvement in the root growth of its associated plants [47]. Recent studies have also proven the hypothesis that bacterially produced IAA contributes toward phenotypic changes in the root architecture of treated plants (**Figure 3**) (**Table 1**) [48–50].

4. Conclusions

Auxin is a key phytohormone controlling the whole physiology of plants by interacting and regulating other phytohormones as well. Besides plants, various rhizobacteria have the ability to produce auxins. Various auxin biosynthetic pathways act simultaneously to regulate auxin formation. These pathways in plants and bacteria are highly similar, however, the tryptophan side chain oxidase pathway is the mechanism found only in bacteria. The main precursor for auxin synthesis is tryptophan, however, tryptophan-independent routes are also present but these routes are not well described and need to be studied. Auxin besides controlling plant growth and development, also affects various regulatory processes in bacteria as well, making inter and intrakingdom cross-signaling interactions. In bacteria, auxin primarily supports bacterial survival by strengthening their stress tolerance mechanism and also enhancing colonizing ability. This also helps in bacterial rhizospheric competence making them more adaptive to the environment. As an interkingdom signaling molecule, auxins interact with various plant signaling mechanisms and coordinate various plant growth processes. Auxins directly affect plant root architecture helping plants for enhanced nutrient and water uptake even under various stress conditions. Plants under optimum auxin levels showed enhanced and prolonged root systems but higher levels of auxin do not increase root length instead initiate the formation of lateral roots and root hair. However, very low auxin levels do not show any effect on root growth. Thus, auxins exert a significant impact (either directly or indirectly) on the healthy development and growth of the plants in a coordinated manner.

Conflict of interest

The authors declare no conflict of interest.

Author details

Aqsa Tariq and Ambreen Ahmed*
Institute of Botany, University of the Punjab, Quaid-e-Azam Campus, Lahore,
Pakistan

*Address all correspondence to: ambreenahmed1@hotmail.com

IntechOpen

References

[1] Kan J, Fang R, Jia Y. Interkingdom signaling in plant-microbe interactions. Science China Life Sciences. 2017;**60**(8): 785-796. DOI: 10.1007/s11427-017-9092-3

[2] Zhao Y. Auxin biosynthesis and its role in plant development. Annu. Rev. Plant Biology. 2010;**61**:49-64. DOI: 10.1146/annurev-arplant-042809-112308

[3] Ludwig-Müller J. Auxin conjugates: Their role for plant development and in the evolution of land plants. Journal of Experimental Botany. 2011;**62**(6):1757-1773. DOI: 10.1093/jxb/erq412

[4] Patten CL, Glick BR. Bacterial biosynthesis of indole-3-acetic acid. Canadian Journal of Microbiology. 1996;**42**(3):207-220. DOI: 10.1139/ M96-032

[5] Spaepen S, Vanderleyden J, Remans R. Indole-3-acetic acid in microbial and microorganism-plant signaling. FEMS Microbiology Reviews. 2007;**31**(4):425-448. DOI: 10.1111/ J.1574-6976.2007.00072.x

[6] Kamilova F, Validov S, Azarova T, Mulders I, Lugtenberg B. Enrichment for enhanced competitive plant root tip colonizers selects for a new class of biocontrol bacteria. Environmental Microbiology. 2005;**7**(11):1809-1817. DOI: 10.1111/j.1462-2920.2005.00889.x

[7] Spaepen S, Vanderleyden J. Auxin and plant-microbe interactions. Cold Spring Harbor Perspectives in Biology. 2011;**3**(4):1-15. DOI: 10.1101/ cshperspect. a001438

[8] Kefford NP, Brockwell J, Zwar JA. The symbiotic synthesis of auxin by legumes and nodule bacteria and its role in nodule development. Australian Journal of Biological Sciences. 1960;**13**(4):456-467. DOI: 10.1071/ BI9600456

[9] Zhang P, Jin T, Sahu SK, Xu J, Shi Q, Liu H, et al. The distribution of tryptophan-dependent indole-3-acetic acid synthesis pathways in bacteria unraveled by large-scale genomic analysis. Molecules. 2019;**24**(7). DOI: 10.3390/molecules24071411

[10] Brown ME, Burlingham LSK. Production of plant growth substances by Azotobacter chroococcum. J Gen Microbial. 1968;**53**(1):135-144. DOI: 10.1099/00221287-53-1-135

[11] Merzaeva DV, Shirokikh IG. The production of auxins by the endophytic bacteria of winter rye. Applied Biochemistry and Microbiology. 2010;**46**(1):44-50. DOI: 10.1134/ S0003683810010072

[12] Kiyohara S, Honda H, Shimizu N, Ejima C, Hamasaki R, Sawa S. Tryptophan auxotroph mutants suppress the superroot 2 phenotypes, modulating IAA biosynthesis in Arabidopsis. Plant Signaling & Behavior. 2011;**6**(9):1351-1355. DOI: 10.4161/psb.6.9.16321

[13] Prinsen E, Costacura A, Michiels K, Vanderleyden J, Van Onckelen H. *Azospirillum brasilense* indole-3-acetic acid biosynthesis: Evidence for a non-tryptophan dependent pathway. Molecular Plant-Microbe Interactions. 1993;**6**(5):609-615. DOI:

[14] Li M, Guo R, Yu F, Chen X, Zhao H, Li H, et al. Indole-3-acetic acid biosynthesis pathways in the plant-beneficial bacterium *Arthrobacter* pascens ZZ21. International Journal of Molecular Sciences. 2018;**19**(2):1-15. DOI: 10.3390/ijms19020443

[15] Ahmad E, Sharma SK, Sharma PK. Deciphering operation of tryptophan-independent pathway in high indole-3-acetic acid (IAA) producing Micrococcus aloeverae DCB-20. FEMS

Microbiology Letters. 2020;**24**:fnaa190. DOI: 10.1093/femsle/fnaa190

[16] Wagi S, Ahmed A. Bacillus spp.: Potent microfactories of bacterial IAA. Peer J. 2019;**7**:e7258. DOI: 10.7717/peerj.7258

[17] Ahmed A, Hasnain S. Extraction and evaluation of indole acetic acid from indigenous auxin-producing rhizosphere bacteria. J. Anim. Plant Sci. 2020;**4**:1024-1036. DOI: 10.36899/JAPS.2020.4.0117

[18] Suliasih WS. Isolation of Indole Acetic Acid (IAA) producing Bacillus siamensis from peat and optimization of the culture conditions for maximum IAA production. In IOP Conference Series: Earth and Environmental Science. 2020;**572**(1):1-12. DOI: 10.1088/1755-1315/572/1/012025

[19] Ahmed A, Hasnain S. Auxin-producing Bacillus sp.: Auxin quantification and effect on the growth of Solanum tuberosum. Pure and Applied Chemistry. 2010;**1**:313-319. DOI: 10.1351/PAC-CON-09-02-06

[20] Vande Broek A, Gysegom P, Ona O, Hendrickx N, Prinsen E, Van Impe J, et al. Transcriptional analysis of the Azospirillum brasilense indole-3-pyruvate decarboxylase gene and identification of a cis-acting sequence involved in auxin responsive expression. Molecular Plant-Microbe Interactions. 2005;**18**(4):311-323. DOI: 10.1094/MPMI-18-0311

[21] Patten CL, Glick BR. Role of Pseudomonas putida indoleacetic acid in development of the host plant root system. Applied and Environmental Microbiology. 2002;**68**(8):3795-3801. DOI: 10.1128/AEM.68.8.3795-3801.2002

[22] Kang BR, Yang K, Y, Cho B. H, Han T. H, Kim I. S, Lee M. C, Anderson A. J, Kim Y. C., Production of indole-3- acetic acid in the plant-beneficial strain Pseudomonas chlororaphis O6 is negatively regulated by the global sensor kinase Gac S. Current Microbiol. 2006;**52**:473-476. DOI: 10.1007/s00284-005-0427-x

[23] Ryu RJ, Patten CL. Aromatic amino acid-dependent expression of indole-3-pyruvate decarboxylase is regulated by TyrR in Enterobacter cloacae UW5. J Bacteriology. 2008;**190**(21):7200-7208. DOI: 109.1128/JB.00804-08

[24] Keswani C, Singh SP, Cueto L, García-Estrada C, Mezaache-Aichour S, Glare TR, et al. Auxins of microbial origin and their use in agriculture. Applied Microbiology and Biotechnology. 2020;**140**:1-17. DOI: 10.1007/s00253-020-10890-8

[25] Persello-Cartieaux F, Nussaume L, Robaglia C. Tales from the underground: molecular plant–rhizobacteria interactions. Plant Cell Environment. 2003;**26**(2):189-199. DOI: 10.1046/j.1365-3040.2003. 00956.x

[26] Scott JC, Greenhut IV, Leveau JHJ. Functional characterization of the bacterial iac genes for degradation of the plant hormone indole 3-acetic acid. Journal of Chemical Ecology. 2013;**39**: 942-951. DOI: 10.1007/s10886-013-0324-x

[27] Patten CL, Blakney AJC, Coulson TJD. Activity, distribution and function of indole-3-acetic acid biosynthetic pathways in bacteria. Critical Reviews in Microbiology. 2013;**39**(4):395-415. DOI: 10.3109/1040841X.2012.716819

[28] Kim JI, Murphy AS, Baek D, Lee S, Yun D, Bressan RA, et al. L (2011a) YUCCA6 over-expression demonstrates auxin function in delaying leaf senescence in Arabidopsis thaliana. Journal of Experimental Botany. 2011;**62**(11):3981-3992. DOI: 10.1093/jxb/err094

[29] Bianco C, Imperlini E, Defez R. Legumes like more IAA. Plant Signaling & Behavior. 2009;**4**:763-765. DOI: 10.4161/psb.4.8.9166

[30] Donati AJ, Lee HI, Leveau JHJ, Chang WS. Effects of indole-3- acetic acid on the transcriptional activities and stress tolerance of Bradyrhizobium japonicum. PLoS One. 2013;**8**:1-11. DOI: 10.1371/journal.pone.0076559

[31] Molina R, Rivera D, Mora V, López G, Rosas S, Spaepen S, et al. Regulation of IAA biosynthesis in Azospirillum brasilense under environmental stress conditions. Current Microbiology. 2018;**75**(10):1408-1418. DOI: 10.1007/s00284-018-1537-6

[32] Van Puyvelde S, Cloots L, Engelen K, Das F, Marchal K, Vanderleyden J, et al. Transcriptome analysis of the rhizosphere bacterium Azospirillum brasilense reveals an extensive auxin response. Microb Ecology. 2011;**61**:723-728. DOI: 10.1007/s00248-011-9819-6

[33] Yang S, Zhang Q, Guo J, Charkowski AO, Glick B. R, Ibekwe A. M. *et al*. Global effect of indole-3-acetic acid biosynthesis on multiple virulence factors of Erwinia chrysanthemi 3937. Appl Environ Microbiology, 2007; 73(4):1079–1088. DOI:10.1128/AEM.01770-06

[34] Phour M, Sehrawat A, Sindhu SS, Glick BR. Interkingdom signaling in plant-rhizomicrobiome interactions for sustainable agriculture. Microbiological Research. 2020;**241**. DOI: 10.1016/j.micres.2020.126589

[35] Zuniga A, Poupin MJ, Donoso R, Ledger T, Guiliani N. Quorum sensing and indole-3-acetic acid degradation play a role in colonization and plant growth promotion of Arabidopsis thaliana by Burkholderia phytofirmans PsJN. Molecular Plant-Microbe Interactions. 2013;**26**(5):546-553. DOI: 10.1094/MPMI-10-12-0241-R

[36] Sukumar P, Legue V, Vayssieres A, Martin F, Tuskan GA, Kalluri UC. Involvement of auxin pathways in modulating root architecture during beneficial plant–microorganism interactions. Plant, Cell & Environment. 2013;**36**(5):909-919. DOI: 10.1111/pce.12036

[37] Ahmed A, Hasnain S. Auxins as one of the factors of plant growth improvement by plant growth promoting rhizobacteria. Polish Journal of Microbiology. 2014;**3**:261-266

[38] Ludwig-Müller J. Auxin and the interaction between plants and microorganisms. Auxin and its role in plant development. 2014:413-434. DOI: 10.1007/978-3-7091-1526-8_18

[39] Duca DR, Glick BR. Indole-3-acetic acid biosynthesis and its regulation in plant-associated bacteria. Applied Microbiology and Biotechnology. 2020: 1-13. DOI: 10.1007/s00253-020-10869-5

[40] Mathesius U. Auxin: at the root of nodule development? Functional Plant Biology. 2008;**35**:651-668. DOI: 10.1071/FP08177

[41] Theunis M. IAA biosynthesis in rhizobia its potential role in symbiosis (thesis). Universiteit Antwerpen, Antwerp, Belgium; 2005

[42] Huo X, Schnabel E, Hughes K, Frugoli J. RNAi phenotypes and the localization of a protein: GUS fusion imply a role for Medicago truncatula PIN genes in nodulation. J Plant Growth Reg. 2006;**25**:156-165. DOI: 10.1007/s00344-005-0106-y

[43] Glick BR. Bacteria with ACC deaminase can promote plant growth and help to feed the world. Microbiological Research. 2013;**169**(1):30-39. DOI: 10.1016/j.micres.2013.09.009.0

[44] Fatima H, Ahmed A. Indole-3-acetic acid synthesizing chromium-resistant bacteria can mitigate chromium toxicity in Helianthus annuus L. Plant, Soil and Environ. 2020;**66**(5):216-221. DOI: 10.17221/581/2019-PSE

[45] Ghosh A, Pramanik K, Bhattacharya S, Mondal S, Ghosh SK,

Ghosh PK, et al. Abatement of arsenic-induced phytotoxic effects in rice seedlings by an arsenic-resistant Pantoea dispersa strain. Environmental Science and Pollution Research. 2021;**28**(17):1-17. DOI: 10.1007/s11356-020-11816-7

[46] Vacheron J, Desbrosses G, Bouffaud ML, Touraine B, Moenne-Loccoz Y, Muller D, et al. Plant growth-promoting rhizobacteria and root system functioning. Frontiers in Plant Science. 2013;**4**:356. DOI: 10.3389/fpls.2013.00356

[47] Ortiz-Castro R, Campos-García J, López-Bucio J. Pseudomonas putida and Pseudomonas fluorescens influence Arabidopsis root system architecture through an auxin response mediated by bioactive cyclodipeptides. Journal of Plant Growth Reg. 2020;**39**(1):254-265. DOI: 10.1007/s00344-019-09979-w

[48] Jochum MD, McWilliams KL, Borrego EJ, Kolomiets MV, Niu G, Pierson EA, et al. Bioprospecting plant growth-promoting rhizobacteria that mitigate drought stress in grasses. Frontiers in Microbiology. 2019;**10**:2106. DOI: 10.3389/fmicb.2019.02106

[49] Batista BD, Dourado MN, Figueredo EF, Hortencio RO, Marques JPR, Piotto FA, et al. C., The auxin-producing Bacillus thuringiensis RZ2MS9 promotes the growth and modifies the root architecture of tomato (Solanum lycopersicum cv. Micro-Tom). Archives of Microbiology. 2021;**23**:3869-3882

[50] Oliveira DAD, Ferreira SDC, Carrera DLR, Serrao CP, Callegari DM, Barros NLF, et al. Characterization of Pseudomonas bacteria of Piper tuberculatum regarding the production of potentially bio-stimulating compounds for plant growth. Acta Amazonica. 2021;**51**:10-19

[51] Chu TN, Bui LV, Hoang MTT. Pseudomonas PS01 isolated from maize rhizosphere alters root system architecture and promotes plant growth. Microorganisms. 2020;**8**(4):471. DOI: 10.3390/microorganisms8040471

[52] Horstmann JL, Dias MP, Ortolan F, Medina-Silva R, Astarita LV, Santarém ER, et al. CLV45 from Fabaceae rhizosphere benefits growth of soybean plants. Brazilian Journal of Microbiology. 2020;**51**(4):1861-1871. DOI: 10.1007/s42770-020-00301-5

[53] Lebrazi S, Niehaus K, Bednarz H, Fadil M, Chraibi M, Fikri-Benbrahim K. Screening and optimization of indole-3-acetic acid production and phosphate solubilization by rhizobacterial strains isolated from Acacia cyanophylla root nodules and their effects on its plant growth. Journal of Genetic Engineering and Biotechnology. 2020;**18**(1):1-12. DOI: 10.1186/s43141-020-00090-2

[54] Maya KCB, Gauchan DP, Khanal SN, Chimouriya S, Lamichhane J. Extraction of Indole-3-acetic Acid from Plant Growth Promoting Rhizobacteria of Bamboo Rhizosphere and Its Effect on Biosynthesis of Chlorophyll in Bamboo Seedlings. Indian Journal of Agricultural Research. 2020;**54**(6):1-7. DOI: 10.18805/IJARe.A-5578

[55] Méndez-Gómez M, Castro-Mercado E, Peña-Uribe CA, Reyes-de la Cruz H, López-Bucio J, García-Pineda E. TARGET OF RAPAMYCIN signaling plays a role in Arabidopsis growth promotion by Azospirillum brasilense Sp245. Plant Science. 2020;**293**(110416). DOI: 10.1016/j.plantsci.2020.110416

[56] Zerrouk IZ, Rahmoune B, Auer S, Rößler S, Lin T, Baluska F, et al. Growth and aluminum tolerance of maize roots mediated by auxin-and cytokinin-producing Bacillus toyonensis requires polar auxin transport. Environmental and Experimental Botany. 2020;**176**: 104064