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**Applied Microbiology and
Biotechnology**

ISSN 0175-7598

Volume 104

Number 20

Appl Microbiol Biotechnol (2020)
104:8549-8565
DOI 10.1007/s00253-020-10890-8

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Auxins of microbial origin and their use in agriculture

Chetan Keswani¹ · Satyendra Pratap Singh² · Laura Cueto³ · Carlos García-Estrada^{3,4} · Samia Mezaache-Aichour⁵ · Travis R. Glare⁶ · Rainer Borriss^{7,8} · Surya Pratap Singh¹ · Miguel Angel Blázquez⁹ · Estibaliz Sansinenea¹⁰

Received: 15 July 2020 / Revised: 31 August 2020 / Accepted: 4 September 2020 / Published online: 12 September 2020
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Abstract

To maintain the world population demand, a sustainable agriculture is needed. Since current global vision is more friendly with the environment, eco-friendly alternatives are desirable. In this sense, plant growth-promoting rhizobacteria could be the choice for the management of soil-borne diseases of crop plants. These rhizobacteria secrete chemical compounds which act as phytohormones. Indole-3-acetic acid (IAA) is the most common plant hormone of the auxin class which regulates various processes of plant growth. IAA compound, in which structure can be found a carboxylic acid attached through a methylene group to the C-3 position of an indole ring, is produced both by plants and microorganisms. Plant growth-promoting rhizobacteria and fungi secrete IAA to promote the plant growth. In this review, IAA production and mechanisms of action by bacteria and fungi along with the metabolic pathways evolved in the IAA secretion and commercial prospects are revised.

Key points

- Many microorganisms produce auxins which help the plant growth promotion.
- These auxins improve the plant growth by several mechanisms.
- The auxins are produced through different mechanisms.

Keywords Indole-3-acetic acid · Plant hormones · Plant growth · promoting bacteria

Introduction

Due to global population demand worldwide, the crop production needs an improvement. In recent decades, the focus on crop production has moved from yield to quality and safety, and more recently sustainability. The prospective use of plant growth-promoting rhizobacteria (PGPR) especially those that produce antimicrobial metabolites against phytopathogens could be a wise choice for the management of

soil-borne diseases of crop plants. PGPR are defined as “bacteria influencing positively the growth and performance of plants” (Mendoza-Hernández et al. 2016). PGPR can improve water and nutrient uptake, and abiotic and stress tolerance. Due to the development of “omics” approaches, the molecular basis of plant-bacteria interaction mechanism which are responsible for physiological changes have begun to be understood. PGPR can promote plant growth by several mechanisms including production of phytohormones (Lambrecht

✉ Estibaliz Sansinenea
 estisansi@yahoo.com.mx

¹ Department of Biochemistry, Faculty of Science, Banaras Hindu University, Varanasi, India

² Department of Mycology and Plant Pathology, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, India

³ Instituto de Biotecnología de León (INBIOTEC), Parque Científico de León, Av. Real, 1, 24006 León, Spain

⁴ Departamento de Ciencias Biomédicas, Universidad de León, Campus de Vegazana s/n, 24071 León, Spain

⁵ Département de Microbiologie Faculté SNV, LMA UFA Sétif 1, Sétif, Algeria

⁶ Bio-Protection Research Centre, Lincoln University, PO Box 85084, Lincoln 7647, New Zealand

⁷ Humboldt-Universität zu Berlin, Institut für Biologie, Berlin, Germany

⁸ Nord Reet UG, Marienstr. 27a, 17489 Greifswald, Germany

⁹ Instituto de Biología Molecular y Celular de Plantas, CSIC-Universitat Politècnica de València, 46022 Valencia, Spain

¹⁰ Facultad De Ciencias Químicas, Benemérita Universidad Autónoma De Puebla, 72590 PueblaPue, México

et al. 2000; Mendoza-Hernández et al. 2016). Phytohormones play a major role in modulating plant growth and development.

Several of these rhizosphere beneficial microorganisms (Patten and Glick 1996; Lambrecht et al. 2000) were proved to be producers of a phytohormone (auxin) identical to that found in plants, indole-3-acetic acid (IAA) (Patten and Glick 1996; Lambrecht et al. 2000; Olanrewaju et al. 2017). For PGPR screening, Etesami et al. (2015) proposed the selection of IAA producers as one of the earliest PGP screened trait.

Auxins are a class of small molecules with the ability to induce growth responses in plants. Auxins were the first plant hormones discovered and studied (Teale et al. 2006). Auxins, as an important group of phytohormones, have implicated in most of the quantitative growth changes that occur during a plant's life cycle (Spaepen and Vanderleyden 2011). The term “auxin” is derived from the Greek word “auxein” meaning “to grow”. Salkowski discovered indole-3-acetic acid (IAA) in 1885 (Enders and Strader 2015).

Indole-3-acetic acid (IAA) is the most common plant hormone of the auxin class and it regulates various aspects of plant growth and development (Spaepen and Vanderleyden 2011). It plays a key role in plant physiology and is involved in cell division, elongation, differentiation, fruit development and phototropic response (Teale et al. 2006; Zhao 2010). Plants are not the only organisms able to produce IAA, but also microorganisms, including bacteria, actinomycetes, filamentous fungi and yeast (Libbert et al. 2006; Limtong and Koowadjanakul 2012; Ruanpanun et al. 2010). Several studies have focused on the role of IAA in plants as well as in plant-microbe interactions; however, the role of IAA in fungi and bacteria and the biosynthetic pathways that these organisms use to synthesize IAA have not been deeply investigated (Rao et al. 2010; Reineke et al. 2008).

Chemically, IAA is a carboxylic acid in which the carboxyl group is attached through a methylene group to the C-3 position of an indole ring. In appearance, IAA is a colourless solid substance, which is soluble in polar organic solvents. IAA stimulates cell elongation by modifying certain cell conditions such as increasing the osmotic contents of the cell, increasing permeability of H₂O into cell and decreasing wall pressure, among others. It inhibits or delays abscission of leaves and induces flowering and fruiting. Originally, scientists believed that IAA was a natural fungal hormone since it was firstly isolated from some fungi such as *Rhizopus suinus*. Later, IAA was isolated from plants (Yu et al. 2014). Additionally, there are other naturally occurring indole derivatives expressing auxin activity (Fig. 1), such as indole-3-ethanol, indole-3-acetaldehyde and indole-3-acetonitrile. Other derivatives can be mentioned, such as indole butyric acid (IBA) which was isolated from maize and potato tuber peel and 1-naphthaleneacetic acid (NAA). It was necessary to search

more metabolically and environmentally more stable acid compounds leading to find 2,4-dichlorophenoxyacetic acid (2,4-D) and 2,4,5-trichlorophenoxyacetic acid (2,4,5-T), both phenoxy herbicides and analogues of IAA. The synthesis of IAA was published by Robert Pokorny in 1941 (Pokorny 1941). William Gladstone Templeman in 1940 published his finding that IAA killed broadleaf plants within a cereal field (Templeman and Marmoy 2008).

In recent years, the development of understanding of IAA signalling pathway search in plants has been truly spectacular. IAA is also a common product of L-tryptophan metabolism produced by several microorganisms including PGPR. The microorganisms isolated from rhizospheric region of various crops have the ability to produce IAA as secondary metabolites when there is a rich supply of substrates. IAA can induce the production of longer roots with increased number of root hairs and lateral roots which are involved in nutrient uptake (Datta and Basu 2000).

IAA is known to be synthesized through several pathways which include shikimate which gives rise to indole ring de novo. Most common route is conversion of L-tryptophan to IAA. IAA is a metabolite derived from Trp by many Trp-dependent (Carreno-Lopez et al. 2000) and Trp-independent (Mohite 2013) pathways in plants and bacteria (Korasick et al. 2013; Tivendale et al. 2014). More than one pathway could be present in a bacterium (Fu et al. 2015). In plants, indole-3-acetamide (IAM), indole-3-pyruvic acid (IPyA), tryptamine (TRA) and indole-3-acetaldoxime pathways are the four Trp-dependent IAA biosynthesis pathways while in bacteria, major IAA biosynthesis pathways are indole-3-pyruvic acid, indole-3-acetamide and indole-3-acetonitrile. Several environmental factors like pH, temperature, osmotic and matrix stress and carbon limitation can modulate the level of production of IAA. IAA formation has also been suggested through hydrolysis of IAA conjugates. *Pseudomonas* sp., *Bacillus* sp., *Klebsiella* sp., *Azospirillum* sp., *Enterobacter* sp. and *Serratia* sp. produce IAA (Singh et al. 2019; Singh et al. 2017). They secrete IAA into the plant's auxin pool interfering with the processes of plant's growth. The change for the plant is related with the amount of IAA that is produced and with the sensitivity of the plant tissue, being the root one of the plant's organs that is most sensitive to changes in IAA. Indeed, IAA has been sprayed over agricultural fields to increase crop yields (Sudha et al. 2012). IAA industry has maintained a relatively steady growth of sales for the past few years with a compound annual growth rate of 7.97% from 2013 to 2016. By 2021, it is expected that market size of IAA will reach US\$ 13.9 million (MarketWhatch 2020; Singh et al. 2016).

It is a real need to understand the mechanisms of auxin production in several microorganisms. The purpose of this review is to show how microbes produce auxin and how microbial auxin drives improvements in several aspects of plant performance.

Fig. 1 The chemical structures of natural and synthetic auxins derived from indole acetic acid. 2,4-dichlorophenoxyacetic acid (2,4-D) and 2,4,5-trichlorophenoxyacetic acid (2,4,5-T), indole butyric acid (IBA), 1-naphthaleneacetic acid (NAA)

PGPR-based plant growth hormones

Recently, Zhang et al. (2019) analyzed 7282 prokaryotic genomes belonging to five phyla prevalent in soil and root environments. The analysis demonstrated that rhizobacteria had very high potential to synthesize IAA based on the genes present. Some PGP bacterial genera which were capable of IAA biosynthesis are shown in Table 1. Analyzing *Acinetobacter* from wheat rhizosphere and *Bacillus* from cucumber rhizosphere, Huddedar et al. (2002) and Chen et al. (2010) demonstrated, respectively, that 21.6 and 16.7% of the isolates produced IAA. Eighty-three percent of rhizobacterial isolates from various plants (Khalid et al. 2004) and 100% from *Brassica juncea* L. (Asghar et al. 2002) produce auxins (Asghar et al. 2002; Khalid et al. 2004). This production is higher from bacteria isolated from rhizosphere soils (Asghar et al. 2002; Khalid et al. 2004) than non-rhizosphere soils (Khalid et al. 2004). It should be noted that *Pseudomonas* strains, producers of IAA, were dominant and were isolated from all the above-mentioned rhizospheres.

Auxins are the most important plant hormones produced by *Azospirillum*, *Bacillus megaterium* and *Pseudomonas* spp. (Babalola 2010). As well as these bacteria isolated from crop rhizospheres, other PGPR isolates from polluted soils were reported for their IAA synthesis capacity. Heavy-metal-tolerant bacteria such as *Serratia*, *Escherichia* and *Enterobacter* also showed plant growth-promoting characteristics, and were able to produce IAA in the presence of heavy metals. Both siderophore-producing (*Escherichia* N16, *Enterobacter* N9 and *Enterobacter* K131) and non-siderophore-producing bacteria (*Serratia* K120 and *Serratia* Mc 119) increased IAA production in the presence of Cu, Pb and As (Mendoza-Hernández et al. 2016), as well as *Arthrobacter pascens* ZZ21, fluoranthene degrading bacteria (Li et al. 2018). Picard and Bosco (2003) demonstrated that the percentage of auxin producers increased with increasing

antimony concentrations. The 222 tested strains were isolated from *Achillea ageratum* L. rhizosphere growing in an abandoned open-sky antimony mine in Tuscany (Italy). Later, Rajkumar et al. (2006) and Rajkumar and Freitas (2008) isolated PGPR *Pseudomonas* sp. from polluted soils from tannery effluents in India and a Serpentine site in Portugal, respectively, and showed their resistance to heavy metals and capacities of producing IAA.

There are other hormones produced by PGPR such as cytokinins and gibberellins (Gupta et al. 2015) that lead to enhanced plant shoot growth and whose interaction with auxins can alter root architecture (Vacheron et al. 2013). Ethylene can also improve both plant stress tolerance and drought stress (Rubin et al. 2017) since PGPR keep the ethylene at certain levels enough to reduce plant growth (Ahemad and Kibret 2014; Pérez-Montañó et al. 2014; Ruzzi and Aroca 2015; Heydarian et al. 2016).

IAA production by gram-negative bacteria

Early reports about IAA production by gram-negative PGPs showed that *Azotobacter* sp. produced indolyl-3-acetic acid in tryptophan supplemented medium (Ahmad et al. 2008). A small amount of IAA in old cultures without tryptophan was also found (Brown and Burlingham 1968). Because of the known capacity to increase yields as inoculants of seeds or roots of crop plants in the Soviet Union, *Azotobacter chroococcum* cultures were screened for IAA biosynthesis. Unfortunately, no compound corresponding to IAA was detected in their supernatants. Lee et al. (1970) and Barea and Brown (1974) screened this auxin in *Azotobacter vinelandii* and *Azotobacter paspali* respectively and detected an authentic IAA spot on the chromatographic paper. *Azotobacter vinelandii* as well as *Azospirillum brasilense* synthesized IAA during their growth in a nitrogen-free medium (Lee et al. 1970; Tien et al. 1979).

Table 1 Reported bacterial PGPR and phytopathogens that produce IAA

PGPR	Agricultural crop	Origin	Reference
<i>Acetobacter diazotrophicus</i>	Chemically defined media		Bastian et al. (1998)
<i>Acinetobacter</i>	Wheat	India	Huddedar et al. (2002)
<i>Aeromonas hydrophila</i>	Tomato	Uzbekistan	Kamilova et al. (2005)
<i>Acinetobacter genospecies</i>	Cereals	Pakistan	Khalid et al. (2004)
<i>Arthrobacter pascens</i> ZZ21	Forest soil	China	Li et al. (2018)
<i>Azospirillum brasilense</i>	Cereals	Pakistan	Lambrech et al. (2000); Khalid et al. (2004)
<i>Azospirillum brasilense</i> Spl3t SR2	Pangola-grass	USA	Tien et al. (1979)
<i>Azospirillum lipoferum</i>	Cereals	Pakistan	Khalid et al. (2004)
<i>Azotobacter</i> spp.	Different crops	India	Ahmad et al. (2008)
<i>Bacillus amyloliquefaciens</i> FZB42 and FZB45	Sugar beet	Germany	Idris et al. (2004)
<i>Bacillus amyloliquefaciens</i> SQR9	cucumber	China	Shao et al. (2015)
<i>Bacillus species</i> PSB10	chickpea	India	Wani and Khan (2010)
<i>Bacillus subtilis</i>	Mustard	India	Zaidi et al. (2006)
<i>Bacillus subtilis</i> FZB37	Sugar beet	Germany	Idris et al. (2004)
<i>Bradyrhizobium japonicum</i>	Bread wheat	India	Shaharoona et al. (2008)
<i>Brevibacillus</i> spp.	White clover	Spain	Vivas et al. (2006)
<i>Burkholderia cepacia</i> 0057	Maize	Cuba	Hernandez-Rodriguez, et al. (2008)
<i>Burkholderia vietnamiensis</i>	Cereals	Pakistan	Khalid et al. (2004)
<i>Enterobacter cloacae</i>	Cereals	Pakistan	Khalid et al. (2004)
<i>Herbaspirillum seropidicae</i>	Chemically defined media		Bastian et al. (1998)
Isolate S87	Cabbages	Pakistan	Asghar et al. (2002)
<i>Klebsiella</i> sp.	Turnip rape	India	Ahemad and Khan (2011)
<i>Mesorhizobium</i> sp.	Chickpea	India	Wani et al. (2008)
<i>Paenibacillus polymyxa</i> strains	Wheat	Germany	Lebuhn et al. (1997)
<i>Paenibacillus polymyxa</i> E681	Winter barley	South Korea	Phi et al. (2008)
<i>Paenibacillus polymyxa</i>	Pepper	South Korea	Phi et al. (2010)
<i>Pantoea agglomerans</i>	Cucumber	Uzbekistan	Kamilova et al. (2005)
<i>Pseudomonas aeruginosa</i> AK2	Rice	India	Kamval (2009)
<i>Pseudomonas fluorescens</i>	Potato	Algeria	Mezaache-Aichour et al. (2012)
<i>Pseudomonas fluorescens</i> CHA0	Tobacco	Switzerland	Oberhansli et al. (1991)
<i>Pseudomonas fluorescens</i> WCS365	Tomato	Uzbekistan	Kamilova et al. (2006)
<i>Pseudomonas jessenii</i> PjM15	Serpentine site	Portugal	Rajkumar and Freitas (2008)
<i>Pseudomonas putida</i> B strain1	Tomato		Gravel et al. (2007)
<i>Pseudomonas putida</i> GR 12-2	Arctic grasses	Canada	Glick et al. (1994)
<i>Pseudomonas</i> sp. NARs9	Amaranth	India	Mishra et al. (2009)
<i>Rhizobium</i> sp.	Pea	India	Ahemad and Khan (2012)
<i>Rhodococcus fascians</i>	Lily crops	Worldwide	Vandeputte et al. (2005)
<i>Serratia marcescens</i>	Pumpkins	India	Selvakumar et al. (2008)
<i>Stenotrophomonas maltophilia</i> AVO63	Avocado	Spain	Pliego et al. (2007)
<i>Streptomyces</i> spp.	Potato	Israel	Manulis et al. (1994)
<i>Streptomyces</i> spp.	Wheat		Aldesuquy et al. (1998)
<i>Streptomyces fradiae</i> NKZ-259	Soil sample	China	Myo et al. (2019)

Gram-negative bacteria produce different amounts of IAA (Table 1). Ahmad et al. (2008) isolated PGP bacteria from

different crops and demonstrated that IAA production was higher in fluorescent *Pseudomonas* isolates, followed by

Azotobacter. Huddedar et al. (2002) selected eight *Acinetobacter* with PGP potential and found that five strains produced IAA during the early stationary phase, one isolate showed maximum IAA production during the log phase and two during the late stationary phase. Induction of IAA production by *Pseudomonas* sp. PsA4 occurred during the stationary phase of culture (Rajkumar et al. 2006). IAA synthesis also varies at different pH. *Acinetobacter* strains belonging to the same species isolated from wheat showed an optimum production at pH 7.0 for some strains (i.e. *Acinetobacter baumannii* A16) and 9.0 for others (i.e. *Acinetobacter baumannii* A13) (Huddedar et al. 2002). Earlier, Oberhansli et al. (1991), studying *Pseudomonas protogenes* CHA0, showed an increase of production with decreasing pH. An acidic pH is typical for the rhizosphere environment due to proton extrusion through membranes of root cells (Spaepen et al. 2007).

Tryptophan is naturally secreted in root exudates of tomato plants and most of the auxin found in the rhizosphere is believed to come from the biosynthesis by microorganisms (Kamilova et al. 2006). Antagonistic *Pseudomonas* sp. PsM6 and PjM15 and growth-promoting strains belonging to the same genera utilized tryptophan (Trp) as a precursor for IAA production (Patten and Glick 1996; Rajkumar and Freitas 2008) and growth (Rajkumar and Freitas 2008). For rhizobacteria from wheat, rice and maize (*Azospirillum lipoferum*, *Acinetobacter genospecies*, *Bukholderia vietnamiensis*, *Enterobacter cloacae*, *Pseudomonas aeruginosa* and *Pseudomonas putida*), IAA biosynthesis may occur in the presence as well as in the absence of tryptophan (Asghar et al. 2002; Khalid et al. 2004). Bacterial IAA is generally synthesized via two pathways, the Trp-independent and the Trp-dependent by sequential conversion of tryptophan to various intermediates.

Trp-independent synthesis

Wright et al. (1991) showed that the non-tryptophan route is the primary pathway for the generation of IAA in maize from detailed analysis using a maize tryptophan auxotroph. This Trp-independent pathway in plants may occur via either indole or indole-3-glycerol phosphate (Persello-Cartieaux et al. 2003). Prinsen et al. (1993), using labelled tryptophan-feeding experiments, reported for the first time an IAA Trp-independent pathway occurring in the nitrogen-fixing rhizobacteria *Azospirillum brasilense* Sp6 and its Tn5 mutant SpM7918. This pathway produced 90% of the IAA in the absence of tryptophan. Recently, Li et al. (2018) speculated the existence of an uncharacterized tryptophan-independent pathway for IAA biosynthesis in the absence of an exogenous tryptophan supply from an endogenous precursor in *Arthrobacter pascens* ZZ21.

Trp-dependent synthesis

Nomenclatures of Trp-dependent biosynthetic pathways are closely related to implied intermediates (Patten and Glick 1996). Of 7282 prokaryotic genomes analyzed by Zhang et al. (2019), 82.2% were potential producers of IAA from tryptophan or its intermediates. Five different pathways of IAA production using tryptophan as a precursor have been identified in gram-negative bacteria, as shown in Fig. 2.

- Indole-3-acetamide (IAM) pathway, in which tryptophan is first converted to IAM by tryptophan-2-monooxygenase and IAM is then converted to IAA by IAM hydrolase. IAM pathway was firstly reported specifically for phytopathogenic bacteria such as *Agrobacterium tumefaciens* and *Pseudomonas syringae* pv. *savastanoi* (Thomashow et al. 1984).
- Indole-3-pyruvic acid (IPyA) pathway, tryptophan is first converted to IPyA by amino transferase (tryptophan transaminase), IPyA is then carboxylated to indole-3-acetaldehyde (IAAld) by indole-3-pyruvic acid decarboxylase (IPDC) and the last step is an oxidation of IAAld to IAA. This pathway was observed in several non-deleterious bacteria (Persello-Cartieaux et al. 2003) including *Rhizobium* (Thomashow et al. 1984; Kobayashi et al. 1995).
- Tryptophan side-chain oxidase (TSO) pathway, tryptophan is directly converted to IAAld prior to oxidation of IAAld to IAA. This pathway was only reported in *Pseudomonas fluorescens* strains, more recently reclassified as *protogenes*, i.e. CHA0 (Oberhansli et al. 1991).
- Tryptamine (TAM) pathway, begins with decarboxylation of tryptophan to TAM, TAM is then converted to IAAld by amine oxidase and then IAAld is converted to IAA by oxidation.
- Indole-3-acetonitrile (IAN) pathway, in which intermediates could be directly converted to IAA by nitrilase or converted to IAM prior to conversion of IAM to IAA by nitrile hydratase.

Kobayashi et al. (1995) suggested that a route involving nitrile hydratase (catalyzing the initial step) and amidase (the later step) rather than nitrilase occurs commonly in plant-associated bacteria for IAA formation from indole-3-acetonitrile, differing from the tryptophan-2-monooxygenase/indole-3-acetamide hydrolase pathway, where nitrile hydratase is inducible by indole acetamide, the intermediate in this pathway. The indole acetonitrile and indole pyruvic acid pathways are also inducible by intermediates or precursors, while the indole acetamide pathway is constitutive in most of the studied microorganisms (Patten and Glick 1996).

Fig. 2 IAA biosynthetic pathways in gram-negative bacteria. Adapted from Spaepen et al. (2007)

Failure to isolate mutants completely deficient in IAA biosynthesis suggests the existence of more than one pathway to IAA production within many organisms (Patten and Glick 1996). *Pantoea dispersa* strain GPK produces IAA from Trp through the IPyA pathway, and acid aminotransferase is highly specific where Trp and α -ketoglutarate are donor and acceptor of the amino group, respectively (Kulkarni et al. 2013a, b), while *Azospirillum brasilense* simultaneously used IAM, IPyA and IAN pathways for IAA biosynthesis from tryptophan (Zakharova et al. 1999). Tryptophan transaminase and TSO activities were detected in CHA0, while Trp transaminase activity was constant throughout the exponential and stationary phases, TSO was only observed during the stationary phase of growth. CHA0 mutant (CHA750) lacking TSO synthesis was able to synthesize the same amount of IAA, presumably using the tryptophan transaminase pathway (Oberhansli et al. 1991). Two IAA biosynthesis pathways in *P. putida* subgroup B strain I have been reported, the tryptophol (TOL) and tryptamine pathways (Gravel et al. 2007). Under low aerobic conditions, enzymes catalyzing the reduction of indole pyruvic acid and indole acetaldehyde to indole acetic acid and indole ethanol (tryptophol), respectively, are activated. Since the reductive reactions are reversible, it is possible that IAA and indole ethanol are storage products involved in the regulation of IAA biosynthesis (Patten and Glick 1996). Li et al. (2018) demonstrated the existence of both IAM and IPyA Trp-dependent pathways in the plant-beneficial rhizobacterium *Arthrobacter pascens*

ZZ21 which is a degrading fluoranthene strain. Moreover, the ability to synthesize IAA from IAM and TAM intermediates is widely distributed in almost all the rhizobacteria analyzed genomes. This also confirmed potentially coexisting pathways in each genome (Zhang et al. 2019).

The effect of bacterial inoculation of radish seeds with *P. fluorescens* strain WCS365, which converted tryptophan to IAA, significantly increased the dry weight of radish roots (Kamilova et al. 2006). *Pantoea dispersa* strain GPK which produces high quantities of IAA increased the root length, shoot length and total dry mass of tested chickpea and pigeon pea plants (Kulkarni et al. 2013a, b). *Serratia* K120 showed a positive correlation between ACC deaminase and IAA in the presence of different types of heavy metals (Cu, Pb, As, Ni, Cr, Cd or Mn). *A. pascens* ZZ21 promotes plant growth and enhances tolerance to fluoranthene by producing IAA, leading to increased fluoranthene uptake by plants, thereby improving plant's ability to remediate fluoranthene-contaminated soils (Li et al. 2018).

Both agrobacteria and rhizobia induce plant cells to proliferate. In many *Rhizobium* species, large plasmids ranging from 90 to 300 MDa encode symbiotic functions such as nodulation, while in *Agrobacterium tumefaciens*, the Ti plasmid encodes enzymes that directs the synthesis of the IAA plant growth regulators (Kobayashi et al. 1995). Genes located in plasmids usually represent higher levels of transcription, as plasmids frequently occur with high copy numbers and can transfer and insert DNA into the plant chromosomes, i.e.

Agrobacterium tumefaciens. The location of IAA biosynthesis genes, either on the plasmid or on the bacterial chromosome, determines levels of IAA production (Patten and Glick 1996). In *Acinetobacter haemolyticus* A19, IAA genes are encoded on the plasmid pUPI126 with resistance to selenium, tellurium and lead (Huddedar et al. 2002). In *Arthrobacter pascens* ZZ21, the presence of genes does not correlate with the biosynthetic pathways in which they are usually involved; *iaaM*-homologous gene was detected, as well as *aam* and *gatA*, which were predicted to encode amidases. However, in response to tryptophan, no significant changes in transcript levels were observed. Studying worldwide strains of phenazine-producing *Pseudomonas* spp., Biessy et al. (2019) demonstrated that every *P. chlororaphis* strain harbours only two IAA biosynthesis genes encoding tryptophan-2-monooxygenase (*IaaM*) and indole-3-acetamide hydrolase (*IaaH*). These genes are located on the chromosome, since no plasmids were detected in the sequenced genomes (Biessy et al. 2019). IAA biosynthesis genes or gene clusters benefit phenazine-producing *Pseudomonas* spp., which colonized the rhizosphere of *Arabidopsis thaliana* and *Solanum tuberosum*, since their presence increases the growth of the plants up to 65 % and 31 %, respectively, more than strains not harboring them (Zboralski et al. 2020).

IAA production by plant growth-promoting Bacilli

While enhancement of plant growth by gram-positive rhizobacteria is well known and commercialized since more than four decades (Broadbent et al. 1977; Fan et al. 2018), the basic molecular principles for this beneficial effect have remained largely hidden for a long time. Early experiments devoted to production of phytohormones by PGPR bacilli led to detecting cytokinin production in *Paenibacillus polymyxa* (Timmusk et al. 1999). Gutierrez-Manero et al. (2001) reported high amounts of gibberellins synthesized in *Bacillus pumilus* and *Bacillus licheniformis*. Synthesis of IAA in gram-positive bacteria was demonstrated at first in *Paenibacillus polymyxa* (Lebuhn et al. 1997), and later in the phytopathogenic actinobacterium *Rhodococcus fascians* (Vandeputte et al. 2005) where it was shown that auxin synthesis contributes to the pathogenic effect (occurrence of leafy galls in infected plants) (Vandeputte et al. 2005).

Culture supernatants of several plant growth-promoting *Bacillus* strains belonging to the *B. subtilis* species complex (Fritze 2004) were able to enhance root elongation growth of maize seedlings in a way corresponding to 10–6 to 10–7 mol/L IAA (Idris et al. 2004). Applying the coleoptile bending test, which permits specific detection of auxin-like compounds (Borriess 1955, 1956), revealed that culture filtrates of FZB37,

FZB42 and FZB45 caused the same specific response on maize coleoptiles as IAA. The fraction containing the auxin-like compounds IAA and indole-3-acetonitrile was enriched by ether extraction at pH 8.5 and pH 3.0, respectively. Furthermore, it was shown that auxins were best produced under low aeration conditions at low temperatures in nutrient-poor media such as Landy or 1C media. ELISA assays with IAA-specific antibodies corroborated the presence of IAA in the fraction further enriched by preparative HPLC. Mass spectroscopy revealed in addition to IAA, indole-3-acetonitrile, a direct precursor of IAA, was also present in the culture filtrate of FZB42.

Bacterial IAA synthesis is known as a mechanism by which beneficial gram-positive rhizobacteria promote plant growth (Keswani et al. 2020). Colonization studies performed with SQR9 and cucumber plants demonstrated impressively that the positive plant growth effect caused by colonization of cucumber roots by SQR9 is due to the enhanced IAA synthesis by the bacterium. Moreover, it was shown that enhanced secretion of tryptophan by the plant roots in the presence of the root-colonizing bacterium stimulated vice versa the IAA production of the bacterium demonstrating a symbiotic interaction of both partner organisms (Liu et al. 2016a).

Using a combined approach of chemical and genetic analyses, it was demonstrated that IAA biosynthesis in FZB42 contributes to the plant growth-promoting effect of the rhizobacterium. Genetic mutants impaired in Tryptophan-dependent IAA synthesis were found less efficient in plant growth promotion than wild type FZB42 (Idris et al. 2007). Addition of tryptophan led to drastic increase of IAA production in FZB42 and insertion mutants in the *trpBA* and *trpED* genes, which are involved in tryptophan biosynthesis pathway, were strongly reduced in their ability to produce IAA, suggesting presence of a tryptophan-dependent pathway of IAA synthesis in FZB42. IAA synthesis was blocked when the *ysnE* gene was disrupted. The gene with unknown function encodes a 151 aa protein bearing a N-acetyltransferase domain. Due to its similarity to IAA acetyltransferase (IAAT) in *Azospirillum brasilense*, it was speculated that the enzyme might be involved in conversion of tryptophan to IAA (Fig. 3).

These findings were corroborated by a more recent study performed with *B. amyloliquefaciens* SQR9, a close relative of FZB42 (Shao et al. 2015). The strongest decrease in IAA biosynthesis (86%) was obtained when the *ysnE* gene was inactivated suggesting that an unknown pathway in which tryptophan is possibly deaminated might be the main pathway of IAA biosynthesis in this group of plant-associated bacilli. In addition, inactivation of two genes, *dhaS* and *yclC*, involved in the indole-3-pyruvic acid (IPyA) pathway of IAA synthesis, resulted also in reduction of IAA synthesis. Separate homologous (SQR9) and heterologous (*B. subtilis* 168) expression of the cloned *ysnE* gene and of the three genes forming the entire IPyA pathway (*patB*, *yclC* and *dhaS*) enhance IAA production in the host strain.

Fig. 3 Simplified scheme of IAA biosynthesis pathways in gram-positive PGPR compiled from data from Idris et al. (2007), Phi et al. (2008) and Shao et al. (2015). The Trp-dependent pathway of IAA biosynthesis via tryptamine (TAM) detected in gram-negative bacteria was omitted since no experimental verification in gram-positive bacteria has been reported. The genes considered being involved in IAA biosynthesis are in italics. They are underlined when knock-out mutations in the genes led to reduced IAA biosynthesis. The *ydcC* gene might correspond to the *ipdc* gene found in gram-negative bacteria and *P. polymyxa* E681. Enzymes involved in the chorismate-dependent pathway of tryptophan biosynthesis: AS, anthranilate synthase; APT, anthranilate

phosphoribosyltransferase; TSA, tryptophan synthase subunit A; TSB, tryptophan synthase subunit B. Enzymes predicted as being involved in the different Trp-dependent pathways of IAA biosynthesis: (1) IAM pathway: TMO, Trp-monooxygenase; IAMH, indole-3-acetamide hydrolase; (2) IPyA pathway: AAT, Trp-amino transferase; IPyDC, indole-3-pyruvic acid decarboxylase; AIDH, indole-3-acetaldehyde-dehydrogenase; (3) Indole-3-acetonitrile (IAN) pathway: IAOD, acetaldoxime dehydratase; Nitrilase, indole-3-acetonitrile nitrilase; (4) predicted pathway of IAA biosynthesis in *B. amyloliquefaciens* (nowadays reclassified as being *B. velezensis*, Fan et al. 2017): IAAT, IAA acetyltransferase encoded by *ydcB* (for more details see text)

Corresponding to SQR9, the plant growth-promoting rhizobacterium (PGPR) *Paenibacillus polymyxa* E681 synthesizes IAA from tryptophan via indole-3-pyruvic acid (IPyA) and indole-3-acetaldehyde (IAAM). The key enzyme in this pathway, IPyA-decarboxylase (IPyDC), was cloned from E681 and expressed as glutathione S-transferase fusion protein in *E. coli*. The IPDC activity of the recombinant protein was demonstrated (Phi et al. 2008). The gram-positive *Rhodococcus fascians* uses also the IPyA pathway as the main route to synthesize IAA (Vandeputte et al. 2005) underlining the important role of the IPyA pathway in gram-positive bacteria. The IPyA pathway of IAA biosynthesis was previously demonstrated to act in gram-negative bacteria (Zimmer et al. 1994) but seems to be uncommon in plants (Mano and Nemoto 2012). In Bacilli, in addition to the uncharacterized pathway dependent on the *ydcB* gene and the IPyA pathway of IAA synthesis, there is also a possible pathway via the indole-3-acetonitrile (IAN) intermediate. The *yhcX* gene encoding IAN nitrilase was found up to 27-fold enhanced when SQR9 colonized cucumber roots (Liu et al. 2016a). Taken together

with the results obtained with gram-positive PGPR *B. amyloliquefaciens* *B. velezensis* and *P. polymyxa*, and the actinobacteria *Streptomyces* spp. and *Rhodococcus fascians*, it was concluded that gram-positive bacteria synthesize IAA mainly by tryptophan-dependent pathways. According to the present, the IPyA pathway, with indole-3-pyruvic acid and indole-3-acetaldehyde intermediates, is the most important method of synthesis occurring in bacilli and actinobacteria, as well. In addition, a hitherto uncharacterized pathway accomplished by a putative IAA acetyltransferase, which is encoded by the *ydcB* gene, seems to dominate in *B. amyloliquefaciens*/*B. velezensis* (Fig. 3).

IAA secreting potential of fungal PGPF

IAA biosynthetic pathways in fungi

Several studies have proven the production of IAA in different fungal species; however, only a few of them have described

the biosynthetic route used to synthesize this phytohormone. IAA can be synthesized via Trp-dependent and Trp-independent pathways, and although both pathways coexist in some organisms, most of the studies have focused on Trp-dependent pathways. Three different Trp-dependent biosynthetic pathways have been described in fungi: indole-3-acetamide (IAM), indole-3-pyruvic acid (IPyA) and tryptamine (TAM) (Bunsangiam et al. 2019; Kumla et al. 2020). To distinguish between them, specific metabolic intermediates of each pathway have been identified in different fungal species.

In vivo and in vitro assays in the mycoherbicide *Colletotrichum gloeosporioides* f. sp. *aeschyromene* were confirmed in the production of IAA, and four different metabolic intermediates were identified in the culture filtrates, indole-3-acetamide (IAM), tryptophol (TOL), indole-3-lactic acid (ILA) and indole-3-carboxylic acid (ICA). The presence of these metabolites suggested that IAA in this fungus is synthesized by two pathways that use Trp as a precursor: the IAM pathway and the IPyA pathway (Robinson et al. 1998). In various phytopathogenic fungi that belong to the genus *Rhizoctonia*, large amounts of TOL were also identified, which is a specific product of the IPyA pathway (Furukawa et al. 1996).

In 2008, some of the genes contributing to the production of IAA were identified for the first time in *Ustilago maydis* basidiomycete. It was found that *iad1* and *iad2* genes encoding two different indole-3-acetaldehyde dehydrogenases were essential for IAA production, as well as *tam1* gene encoding a Trp aminotransferase. These enzymes belong to the IPyA biosynthetic route, which suggests that *U. maydis* mainly produces IAA via IPyA pathway (Reineke et al. 2008). This ability to synthesize IAA from Trp via IPyA pathway was also found in *Ustilago esculenta* and *U. scitaminea* (Tzeng 2004).

The IAA biosynthetic pathways were also analyzed in the plant pathogen *Fusarium delphinoides* strain GPK, a causal agent of wilt in chickpea. Analysis of the culture filtrates showed the presence of metabolic intermediates of IPyA and TAM pathways (Kulkarni et al. 2013a, b). Biosynthesis of IAA via IPyA pathway was also found in most ectomycorrhizal fungi (Krause et al. 2015; Kumla et al. 2020) and in several types of yeast (Bunsangiam et al. 2019). However, recent studies have suggested the presence of a Trp-independent pathway for IAA synthesis in many yeast species (Rao et al. 2010; Sun et al. 2014). A mutant *Saccharomyces cerevisiae* strain with deletions in *ald2* and *ald3* genes, which are the homologs of *iad1* and *iad2* genes in *U. maydis*, was able to produce IAA in the absence of exogenous Trp and at higher levels than the wild type, thus suggesting that *S. cerevisiae* may have at least one pathway that is not Trp-dependent (Rao et al. 2010).

Most of the studies on IAA biosynthetic pathways showed the IPyA pathway as the most common pathway found in fungi, and only one example of a Trp-independent biosynthetic process was described so far in *S. cerevisiae* (Rao et al. 2010).

Effects of fungal-produced IAA on fungal-plant interactions

The interest in the interactions of plants and their associate microorganisms, such as fungi, has recently increased because of the importance of these interactions in agricultural practices. Plants produce several organic compounds that are used as nutrients by fungal community (Ortiz-Castro et al. 2009), whereas fungi synthesize siderophores, volatile compounds and phytohormones, which have different effects on plant growth (Keswani et al. 2019a; Haas 2014; Keswani et al. 2014). An extensive communication is established between plants and fungi through these compounds at different stages of plant growth. The coordination of these cellular processes involved in the dialogue between plant and fungi determines the final outcome of the relationship, which ranges from symbiosis to pathogenesis (Bais et al. 2004). In both cases, fungi have to penetrate their plant host without disrupting plant cell inner membrane. Plants are able to detect fungi by their surface receptors, and this stimulates different responses in the plant, such as the activation of their basal immunity in order to protect them from a possible fungal infection (Gust et al. 2012). However, fungi have also evolved to produce different compounds to avoid this immunity and to create a suitable environment to favour their invasion of plant tissues (Kamoun 2007). Some of these fungal compounds are hormones that are also produced by plants to control and regulate their development and growth, such as IAA (Teale et al. 2006; Zhao 2010). These fungal-derived molecules could have a dual role; they could have a beneficial or harmful effect over the plant to favour nutrient uptake and invasion (Gust et al. 2012) or they could act as signals for the fungi themselves (Gruen 1959; Ulrich 2006).

Recent findings on the role of fungal-produced IAA in plant-fungal interactions suggest that fungi may use IAA to favour their colonization of plant tissues, leading to plant growth stimulation and alteration of plant defence mechanisms (Contreras-Cornejo et al. 2009; Prusty et al. 2004).

Maize plants (*Zea mays*) inoculated with the IAA-producing yeast *Candida tropicalis* SSm-39 showed an 85% improvement in grain quality compared with uninoculated controls (Mukherjee and Sen 2015). The fungal-produced IAA promoted the growth and yield of maize; consequently, the dose of chemical fertilizer applied was reduced. This promoting effect was also observed when rice seedlings were inoculated with *C. tropicalis* HY (CtHY), showing superior root growth and an increase of 16–35% in dry weight

compared with uninoculated controls (Amprayn et al. 2012). *Ustilago esculenta* (strain JYC070) is a IAA high-producing strain, and its co-cultivation with *Arabidopsis* seedlings caused a 10-fold increase in the lateral root number compared with those co-cultivated with a low IAA-producing strain (Sun et al. 2014). The IAA synthesized by *Mortiella* species grown under IAA-producing conditions showed a promoting effect on winter wheat seedling growth, resulting in an increase of about 40% and 24% in root and shoot fresh, respectively (Ozimek et al. 2018).

In addition, fungal-produced IAA can indirectly affect plants by boosting plant immune responses to reduce pathogenic strains and disease development (Jogaiah et al. 2013; Radhakrishnan et al. 2013; Verma et al. 2011).

Studies have shown that fungal-produced IAA can regulate plant gene expression and antioxidant homeostasis in order to reduce pathogen infection, as occurs in sesame plants, where the IAA produced by *Penicillium* sp. NICS01 promoted sesame plant growth and suppressed *Fusarium* sp. infection (Radhakrishnan et al. 2013). Another example was documented in tomatoes, which reported a reduction in the infection caused by the *Ralstonia solanacea* bacterium due to the IAA produced by *Trichoderma*. It was observed that the fungal-produced IAA triggered the production of defence-related enzymes and the expression of genes to circumvent the bacterial infection (Jogaiah et al. 2013).

These examples suggest that exogenous treatment with fungal-produced IAA could be used in plants to prevent diseases caused by pathogens; however, the induction of these defence mechanisms caused by IAA may depend on host-pathogen and host-fungi specificities. Therefore, further research on this topic would help understand the role of fungal-produced IAA in plant defence mechanisms.

Fungi and plant roots can establish a symbiotic association. In this kind of association, the fungus colonizes root tissue intracellularly, forming arbuscular mycorrhizae (AM), or, extracellularly, as ectomycorrhizal fungi. Plants supply organic molecules to fungi, such as sugar, whereas fungi supply to the plant water and mineral nutrients taken from the soil, establishing a mutualistic association. The most common symbiotic association is the arbuscular type, present in 70% of plant species (Harrison 2005). Several studies suggest that phytohormones, such as IAA, act as signals in the establishment of AM symbiosis. Accumulation of transcripts for IAA synthesis enzymes was found in tomato plants colonized by arbuscular mycorrhizal fungus (Fiorilli et al. 2009). The discovery of the microRNA 393 evidenced the requirement of auxin signalling during symbiosis. It was found that an overexpression of this microRNA caused a reduction in the expression of auxin receptors resulting in an underdevelopment of arbuscular formation in three different plant species. This result showed that microRNA 393 targets several auxin receptors acting as negative regulator or arbuscular formation (Etemadi et al. 2014).

Although the mechanisms behind the establishment of AM symbiosis remain unclear, it shows a clear role of auxins signalling during the process.

Fungal-produced IAA does not always trigger positive effects on plants. *Arabidopsis* seedlings inoculated with different concentrations of IAA produced by *Trichoderma virens* showed a dose-dependent effect in biomass production. Small amounts (nM range) of IAA increased yield, but higher amounts (mM range) repressed growth (Contreras-Cornejo et al. 2009). This study showed that the inoculation effects of IAA-producing fungi in plants may depend on the concentration and plant species. Several lines of evidence have also suggested that fungal-produced IAA is involved in pathogenic processes. For example, in *S. cerevisiae* and *Candida albicans*, IAA induces morphological transition into hyphal growth, which is a virulence trait (Rao et al. 2010). High levels of fungal-produced IAA were found in plants during the infection of the pathogenic fungus *C. gloeosporioides* f. sp. *aeschynomene*. This pathogen induced epinasty and leaf deformation in *Aeschynomene virginica*, symptoms that were also observed when the plant was treated with IAA (Maor et al. 2004; Robinson et al. 1998). *Fusarium* transgenic strains overexpressing genes involved in IAA biosynthesis showed a hypervirulent phenotype on *Orobanche* (Cohen et al. 2002).

Data from these studies suggest that fungal-produced IAA may have a key role on plant pathogenesis during disease development. Two different mechanisms have been described to explain how this fungal-produced phytohormone could contribute to plant pathogenicity: (i) IAA could inhibit salicylic acid (SA)-dependent defence signalling; it could disrupt the cell wall and open stomata and (ii) IAA may induce plant endogenous IAA biosynthesis, increasing the virulent effect caused by fungal-produced IAA (Fu et al. 2015). However, further studies are needed to deeply understand the mechanisms behind the effect of IAA in the enhancement of the virulence of fungal pathogens in plants.

Effects of fungal-produced IAA on fungal-fungal interactions

Several studies have been carried out to assay the role of IAA on the interactions between fungi. The effect of an exogenous IAA treatment on yeasts, collected from leaf samples of *Drosera indica* L., was evaluated. *U. esculenta* growth was not affected by any tested IAA concentration; however, the growth of 11 from 12 yeasts was significantly inhibited by a high IAA concentration (5000 μ M) (Sun et al. 2014). Similar effects have been described for the plant pathogen *F. delphinoides*, where low concentrations of exogenous IAA promoted the pathogen growth, but high IAA concentrations reduced it (Kulkarni et al. 2013a, b). The effects of different exogenous IAA concentrations were also assayed on *S. cerevisiae* and *S. paradoxus* growth; exogenous added

IAA exerted stimulatory and inhibitory effects on yeast growth depending on its concentration. Furthermore, it was found that yeast species able to synthesize high amounts of IAA were more tolerant when exposed to exogenous IAA. The authors suggest that, since the optimal concentration of IAA for growth is different for each fungus, secretion of IAA may be a crucial factor for fungi to increase their competitiveness. Yeast-produced IAA could inhibit the growth of specific strains competing for the same resources, but in some cases, the produced IAA could stimulate growth of other fungal species or their own growth. This strategy would allow fungi that occupy the same niche to establish an interference competition for resources (Liu et al. 2016b).

The production of IAA has also been associated with quorum sensing. Quorum sensing is the capacity to modulate gene expression according to cell population density (Parsek and Greenberg 2005; Waters and Bassler 2005). According to this definition, it has been found that a cell density-dependent IAA accumulation exists in *S. cerevisiae*, and also that IAA was taken up by yeast through a specific transport system. IAA promotes the transition to filamentous growth in *S. cerevisiae*, increasing its invasion capacity (Prusty et al. 2004). Similar to *S. cerevisiae*, in *C. albicans*, IAA induced hyphal growth; this morphological transition also being controlled by cell density. This morphological switch is considered a virulence factor promoting macrophage evasion, tissue invasion and biofilm formation (Sudbery 2011; Vedyappan et al. 2013). These results show that IAA can function as a diffusible signal used for communication between species, thus allowing the production, transfer and perception of IAA signals between organisms (Fu et al. 2015).

This fungal phytohormone, also produced by plants, can promote plant growth by different mechanisms. Fungal-produced IAA not only stimulates a better root system formation, enhancing water and nutrient absorption (Amprayn et al. 2012; Mukherjee and Sen 2015; Ozimek et al. 2018), but also boosts plant defence response in order to minimize infections caused by pathogenic agents (Jogaiah et al. 2013; Radhakrishnan et al. 2013; Verma et al. 2011). These positive effects caused by fungal-produced IAA could be exploited by agricultural industry. Fungal-produced phytohormones harbour the greatest potential for large-scale production and can be developed into the next generation of green fertilizers for agricultural applications (Wong et al. 2015).

Mechanism of action of microbially secreted IAA

The mechanism of action of auxins in plants is through control of cell division, differentiation, elongation and apical dominance, which results in effects on plant growth (Goswami et al. 2016). By contrast, the mechanisms of action of

microbially produced IAA are not fully understood, especially given the many microorganisms that produce IAA and the different phenotypic and ecological outcomes found. However, similar to auxins in plants, much of the research has focused on how IAA is influencing gene expression.

IAA biosynthesis appears to have evolved independently in bacteria, microalgae, fungi and plants (Fu et al. 2015). While there are a number of studies on bacteria, less is known about fungal IAA biosynthetic pathways and there are few studies on the role of IAA in fungal ecology (Fu et al. 2015). Bacteria producing IAA can cause a variety of outcomes for plants colonized, from pathogenesis to phytostimulation (Spaepen et al. 2007). IAA produced by microbes commonly seems to be involved in the colonization of the plant, whether as part of a pathogenic or commensal process.

Bacterial rhizosphere colonizers, such as *Pseudomonas* and *Rhizobium* spp., have been shown in some cases to stimulate plant growth (Gravel et al. 2007) and also produce IAA. PGPRs produce IAA in the rhizosphere of plant roots, so often roots are the relatively more affected structures. Most Rhizobia can produce IAA and nodule formation in host plants is dependent on changes in auxin balance (Jameson 2000; Mole et al. 2007). Therefore, IAA production is likely to play a role in nodulation, but the exact mechanism is yet to be determined (Spaepen et al. 2007). Reports have linked the effects to altering the auxin balance in plants (Jameson 2000; Mole et al. 2007). The effects of microbial-produced IAA can include root elongation (Myo et al. 2019) branching or increases in size and weight. There is also a suggestion that IAA induces stem tissue to differentiate into root tissue (Goswami et al. 2016). In general, this is thought to improve nutrient exchange, hence promote growth.

However, the effects of IAA are dose-dependent and production of large amounts by microbes can inhibit root growth rather than promote (Xie et al. 1996; Raut et al. 2017). Studies report different findings in relation to the effect of concentrations, with high levels sometimes promoting positive root growth effects as well (Tanimoto 2005). The interactions appear to be microbe-plant specific. The sensitivity of the host to auxins also varies (Spaepen et al. 2007). Xie et al. (1996) found that an IAA overproducing mutant of *Pseudomonas putida* inhibited the root elongation of canola seedlings. It is possible such effects are attributable to ethylene production (Glick et al. 1997, 1998), as IAA is known to increase ACC synthase, which can trigger catalyzation of a precursor to ethylene in plants (Kende 1993).

Interestingly, exogenous application of IAA to pepper plants increased the amount of phosphorus in the roots (San-Francisco et al. 2005), which Gravel et al. (2007) suggested could account for the increase in phosphorus in tomato plants where *P. putida* and *Trichoderma atroviride* were present, as both species produce IAA.

Recently, a lot of focus has been on microbial-produced IAA as a signalling molecule, especially in bacteria (Spaepen et al. 2007). IAA has been shown to affect gene expression in some microbes, acting as an effector molecule (Fu et al. 2015). Plant colonizing bacteria upregulate auxin signalling in plants. There is evidence that IAA as a signalling molecule can interfere with plant defence systems such as pathogen-associated molecular patterns (PAMPs) and mediate defence response. Spaepen et al. (2007) suggested bacterially produced IAA was part of the colonization strategy, that by stimulating proliferation of plant tissues they were able to enhance colonization and obtain more nutrients. They further hypothesize that bacterial IAA may help to evade the host defence system by derepressing auxin signalling in the plant. Fungal-excreted IAA may induce systemic resistance in plants, increasing resistance to plant pathogens (Hermosa et al. 2012). This changing of gene expression by fungal IAA has been demonstrated for *Penicillium* in sesame plants (Radhakrishnan et al. 2013). Dobbelaere et al. (1999) found that mutants with altered IAA production showed a dose response effect that correlated with increasing root growth. However, in several studies with bacteria, IAA production alone did not account for all growth promotion effects on plants, suggesting other compounds are involved (e.g. Xie et al. 1996). As a signalling molecule, IAA may be linked with quorum sensing and other microbial biochemical pathways.

Many microbes also degrade IAA (Donoso et al. 2017), suggesting another role of microbes in IAA effects. IAA production and degradation are likely involved in the ecology of microbes and how they related to the external environment. For example, yeast growth could be inhibited or promoted by differing concentrations of exogenous IAA (Fu et al. 2015).

IAA/auxin synthesis occurs mostly in the shoot apex and then transported to the root apical meristem through the shoot vascular cambium and accumulates in the quiescent centre (QC), and lateral root cap (Brunoud et al. 2012; Petrášek and Friml 2009). There is control of primary root development by the stem cell niche during embryogenesis. Mitigation of cytokinin sensing in the transit zone regulates PINs negatively releasing of auxin again. The efflux of auxin causes differentiation to be initiated again in the cell (Marhavý et al. 2011).

Commercial prospects

The soil is rich in microorganisms with capacity to promote plant growth. These microorganisms are plausible candidates for sustainable agriculture; however, it is necessary to realize safety testing ensuring that these microbes to have not any form of deleterious effects on local environments or human health protecting exposed personnel, environment and management of hazardous secondary

effects (Keswani et al. 2019b). The advantages of microbially produced (IAA) over synthetically produced auxins can be studied by examining the effect of natural and synthetic auxin on the growth and metabolism of green microalga *Chlorella vulgaris*. The experiment concluded *C. vulgaris* when treated with IAA had the highest increase in protein content. IAA had the most stimulatory effect on chlorophyll A and carotenoid while other auxins showed lower stimulatory effects. The enhancement in monosaccharides content was highest in *C. vulgaris* treated with IAA whereas algae treated with synthetic auxins showed the lowest activity. The level of antioxidants like ascorbate and glutathione was increased in the presence of IAA in comparison with other auxins. Algal exposure to IAA showed highest enhancement of the activity of antioxidant enzymes while those treated with synthetic auxin were characterized by weaker influence on the activity of antioxidant enzymes. Lipid peroxides and peroxide concentration were found to be lowest when treated with IAA as compared with other auxins that help in increasing the level of ROS scavenging metabolites and antioxidant enzyme activity (Piotrowska-Niczyporuk and Bajguz 2014).

To develop PGPR or signal compound-based products, proper formulations must be developed for distribution in the field. Liquid and solid inoculants have been developed. After development of the proper formulation to reach the marketplace, it is necessary to have registration approval. Currently, the regulatory procedures for registration and commercialization of bio-stimulants are complex (Backer et al. 2018). The growing population has resulted in increased demand for the food production and is dependent on healthy plants which leads to high crop yield. This is a key factor to be considered for the enormous growth of IAA market. Although the compound is produced naturally, the synthesis has led to improved plant quality resulting in positive impacts. However, the toxicity of the synthetic compound is very high and using without safety and precautions can lead to skin, eyes and respiratory irritation to farmers which limits demand. Despite these serious safety concerns, the products have still maintained a positive sales growth for the past 4 years with an average growth rate of 7.9% from US\$ 8.5 million in 2013 to US\$ 10.7 million in 2016. It is estimated by analysts that by 2021, the market size of IAA will reach US\$ 13.9 million (MarketWhatch 2020).

There are today several examples for commercial products based on IAA: I5148 Indole-3-acetic acid sodium salt (> 98%) manufactured by Sigma-Aldrich is commercially marketed as Bioreagent, suitable for plant cell culture. Similarly, Seradix B No1, Seradix B No 2 and Seradix B No 3 are chemically 4-indol-3-yl-butyric acid manufactured by Bayer. ProGibb 4% (gibberellin) and Promalin (cytokinin) are manufactured by Valent Biosciences.

Conclusion

There is an urgent need to develop technologies and sustainable agricultural approaches to increase food production, due to the rapidly increasing population and loss of productive land. One approach that might be undertaken is the more widespread use of PGPB instead of agricultural chemicals. However, in order to make this approach possible, new and improved techniques for large-scale production, formulation, storage, shipping and application of PGPB need to be developed. Inconsistent results in field application of biologicals still hinder their successful use by the farmers. Detailed studies on mechanisms by which signals perceived by hormone receptors that are transmitted are urgently needed. The growth of more than 90% of all plants is enhanced by mycorrhiza fungi, so it is important to study the interaction between PGPB and mycorrhiza and to understand the mode in which they can promote growth and development of plants. More research is also required on PGPF modulating levels of plant hormones so that they can be effectively used in promoting plant growth and development.

Contributors All the authors have contributed equally, have read and approved the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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