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REVIEW
BIOSYNTHESIS OF INDOLE-3-ACETIC ACID AND PLANT GROWTH PROMOTING BY BACTERIA

Revisión bibliográfica
Biosíntesis de ácido indol-3-acético y promoción del crecimiento de plantas por bacterias

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ABSTRACT. The plant hormone indole-3-acetic acid (IAA) is the main auxin in plants. IAA controls several physiological processes such as cell elongation and division, tissue differentiation and responses to light and gravity. IAA concentration is regulated in plants. Interestingly, bacteria can modulate IAA levels. The most widely distributed biosynthetic IAA routes in bacteria are indole-3-pyruvate (IPA) and indole-3-acetamide (IAM) anabolic pathways. These metabolic pathways use tryptophan as precursor. IPA pathway has been described mainly in plant growth-promoting bacteria (PGPB), whereas the IAM pathway is present in phytopathogenic bacteria. PGPB stimulate plant growth through various mechanisms including the production of plant hormones. Studies on PGPB that are capable to produce IAA indicate that this phytohormone plays a crucial role for promoting plant growth.

Key words: indole acetic acid, auxin, bacteria, phytohormone, plant, tryptophan

RESUMEN. La hormona vegetal ácido indol-3-acético (AIA) es la principal auxina en las plantas. El AIA controla diversos procesos fisiológicos como la elongación y división celular, la diferenciación de tejidos y las respuestas a la luz y la gravedad. La concentración de AIA se encuentra regulada en las plantas. Se ha descrito que las bacterias pueden modular los niveles de AIA. Las rutas biosintéticas de AIA más importantes y ampliamente distribuidas en bacterias son las vías anabólicas de indol-3-piruvato (IPA) y de indol-3-acetamida (IAM). Estas rutas metabólicas son dependientes del precursor triptófano. La vía IPA ha sido descrita principalmente en bacterias promotoras del crecimiento (PGPB), mientras que la vía IAM está presente en bacterias fitopatógenas. Las PGPB estimulan el crecimiento de las plantas mediante diversos mecanismos, que incluyen la producción de fitohormonas. Diversos estudios sobre PGPB que poseen la capacidad de producir AIA demuestran que esta fitohormona juega un rol determinante en la promoción del crecimiento vegetal.

Palabras clave: ácido indolacético, auxina, bacteria, fitohormona, planta, triptófano

INTRODUCTION

Vegetable Hormones

Pioneering studies in the XIX century by Julius von Sachs and Charles Darwin showed that various plant growth processes were regulated by "substances" transported from one part of the plant to another (1). More than a century later, these substances are known to be structurally unrelated small molecules that derive from essential metabolic vias of plants. In general, these compounds are present in very low concentrations and act locally, around the site of synthesis or in distant tissues. New plant hormones, including auxins such as indole-3-acetic acid (IAA), abscisic acid (ABA), brassinosteroids (BRS), cytokinins, gibberellins, ethylene, jasmonic acid (JA) and Salicylic acid (SA) (Figure 1). Auxins, cytokinins, ABA, ethylene, salicylic acid and gibberellins can also be produced by bacteria (2, 3, 4, 5, 6, 7). These hormones regulate all aspects of plant life, from pattern formation during development to responses to biotic and abiotic stress (8, 9)
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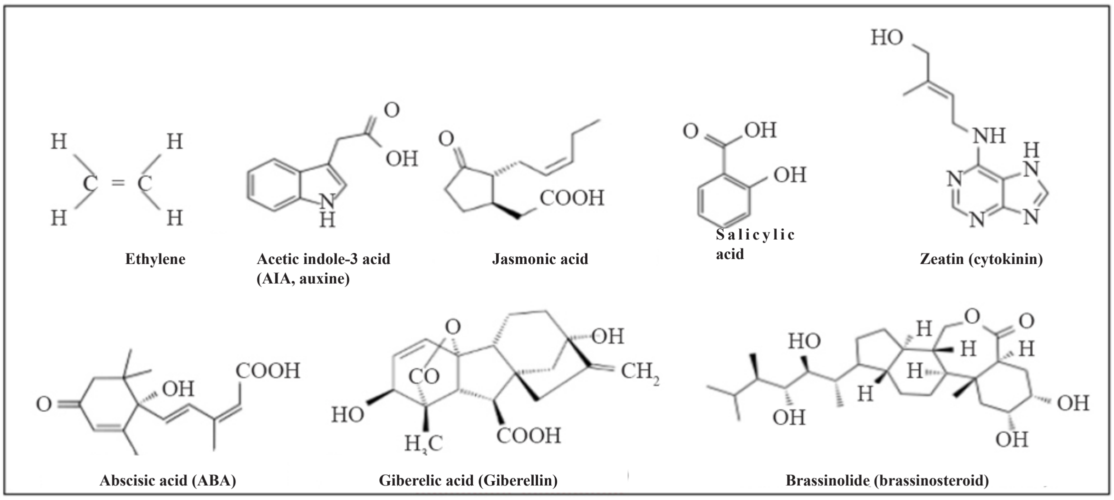


Figure 1. Chemical structure of plant hormones

A partial list of the responses of each phytohormone is described below (8). Ethylene gas promotes fruit maturation, senescence, response to pathogens and abiotic stress. IAA (auxin) regulates cell division and expansion, vascular differentiation, lateral root development, and apical dominance. Jasmine acid is a volatile signal that modulates pollen development and responses to pathogen infections. Salicylic acid is involved in the growth and development of the plant, in mechanisms of resistance to phytopathogens, and in responses to abiotic and biotic stress (10). Cytokinins are adenine derivatives identified by their ability to promote cytokinesis. Abscisic acid promotes seed latency and participates in several stress signaling vias. Gibberellins are diterpenoid compounds that promote germination, stem elongation and induction of flowering. The brasinoesteroids regulate cell expansion and photomorphogenesis.

Auxins

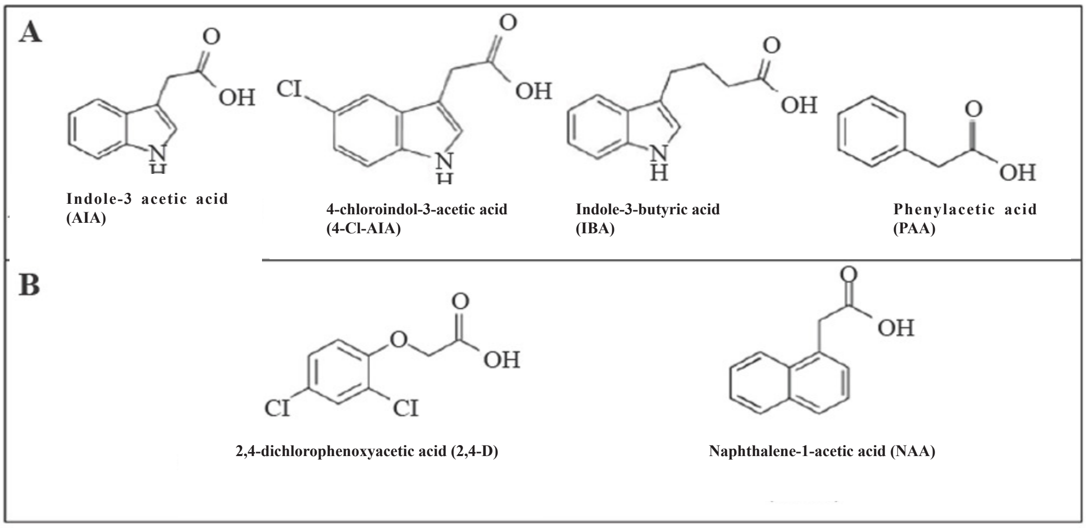
Auxins are plant growth hormones due to their ability to stimulate differential growth in response to light stimuli (11). They are the phytohormones that play the most important role in the development of plants (12). Four auxins synthesized by plants have been described: IAA, indol-3-butyric acid (IBA), 4-chloroindole-3-acetic acid (4-Cl-IAA) and phenylacetic acid (PAA) (13) (Figure 2A). *In vitro* tests have made it possible to determine that IAA is one of the main auxins involved in plant development (14,15). The agrochemical industry has developed synthetic auxins that mimic the structure of EIA. Synthetic auxins most widely used as herbicides are 2,4-dichlorophenoxyacetic acid (2,4-D) and naphthalene-1-acetic acid (NAA) (13) (Figure 2B). In contrast to IAA, these herbicides have a long median life, due to their high stability in higher plants and, therefore, greater effectiveness than IAA. At low concentrations they are able to stimulate the processes of development and growth of plants, but at high concentrations the growth is disturbed and the plant is damaged causing its death (16, 17).

Acid indole-3-acetic acid (IAA)

The IAA is the main native auxin of the upper plants (14). The IAA is involved in the growth and development of plants, mainly in a series of physiological processes that include cell elongation and division, tissue differentiation, phototropism, gravitropism and in defensive responses (9, 18), highlighting an important role in The formation of the xylem and the root (19). IAA biosynthesis is not limited to higher plants. Organisms such as bacteria, fungi and algae are able to synthesize IAA, which can affect the growth and development of plants (20). In bacteria, the production of IAA is a relevant capacity of both PGPBs and phytopathogenic bacteria (21, 22). The higher plants exude, among other components, the amino acid tryptophan, which is the main precursor for microbial IAA biosynthesis (23, 24, 25, 26).

Biosynthesis of IAA in Bacteria

It has been proposed that 80 % of the bacteria in the rhizosphere are capable of producing IAA. A high degree of similarity has been observed in the IAA synthesis vias of plants and bacteria (27).



A: natural auxins B: Auxins produced by industrial chemical synthesis

Figure 2. Auxin diversity

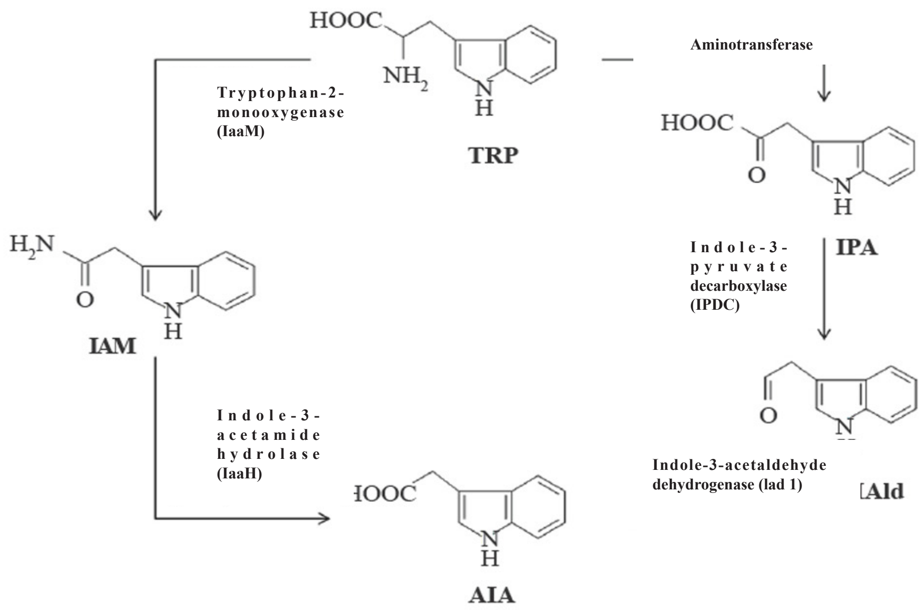
The rhizosphere microorganisms that interact with the plants interfere with their development by the auxin imbalance, so that they can affect the plant in a positive or negative way (7). IAA-producing bacteria (BIP) have the potential to interfere with the processes of incorporation of IAA into plants. The consequence for the plant depends on the amount of IAA produced and the sensitivity of the plant tissue to changes in the concentration of IAA (18), which is associated with the biosynthetic via used by the bacteria associated with plants (27). Phytopathogenic bacteria such as *Agrobacterium* spp. and *Pseudomonas savastanoi* pv. *Savastanoi* cause in the plant tissue tumors and crown of galls, respectively, which in young plants mean growth retardation, abnormal development, susceptibility to other diseases or death of the plant (28, 29). On the other hand, the PGPB *Azospirillum* favors the development of the root (27, 30). Tryptophan is the main precursor in bacterial IAA biosynthetic vias (27, 31). Different vias of IAA synthesis have been identified in bacteria. Five plants of these anabolic vias are tryptophan-dependent. The most important and widely distributed IAA synthesis vias are the indole-3-pyruvate (IPA) via and the indole-3-acetamide via (IAM) (7). The IPA via has been reported mainly in PGPB, whereas the IAM via has been described in phytopathogenic bacteria (7, 27) (Figure 3). In addition, tryptophan-independent IAA synthesis vias have been described, which have been studied by mutants and isotopic labeling. These anabolic vias in the presence of tryptophan significantly increase the production of IAA (20). The amino acid tryptophan is one of the main components of root exudation (26). IAA bacterial biosynthesis can contribute to bacterial survival by detoxification of tryptophan from exudate of plants (27).

Via indole-3-pyruvate (IPA)

The IPA via has been proposed as the main route for IAA biosynthesis in plants. However, key enzymes or genes have not yet been identified in plants (7). The production of EIA by the IPA has been described in various bacteria, such as the phytopathogen *Pantoea agglomerans*, beneficial bacteria (e.g., *Bradyrhizobium, Azospirillum, Rhizobium and Enterobacter cloacae*) and in cyanobacteria. This via has as the first step the conversion of tryptophan to indole-3-pyruvic acid (IPA) by an aminotransferase. In a second step the IPA is decarboxylated to indole-3-acetaldehyde acid (IAAld) by indole-3-pyruvate decarboxylase (IPDC), which is the limiting step of the synthesis. The ipdCque gene encoding the enzyme IPDC has been characterized in some bacteria such as *Azospirillum brasilense*, *E. cloacae*, *Pseudomonas putida*, *P. Agglomerans* and *Paenibacillus polymyxa* (22, 27, 32). In the final step, the IAAld is oxidized to IAA by indole-3-acetaldehyde dehydrogenase (7, 27).

Via indole-3-acetamide (IAM)

The IAM via is the most characterized via in bacteria. This via has not been described in plants (27). This metabolic via is present in various pathogens and contributes to the virulence of these bacteria by the excessive production of IAA (28, 30). The phytopathogenic symptoms are mainly linked to the IAM via, since it would be specifically microbial (27)



right side , vía indol-3-piruvato (IPA) lado izquierdo, vía indol-3-acetamida (IAM) TRP: triptófano AIA: ácido indol-3-acético IPA: ácido indol-3-pirúvico AIAld: Indole-3-acetamide hydrolase (IaaH) IAM: indol-3-acetamida.

Figure 3. Indol-3-acetic acid biosynthesis vias in bacteria

because plants do not possess the metabolic intermediates of this via, they are not able to maintain IAA at non-toxic or physiologically appropriate levels in their tissues by feedback (30). The genes, proteins and regulation of this metabolic via have been characterized and comprise two stages. In the first, tryptophan is converted to IAM by the enzyme tryptophan-2-monooxygenase (IaaM), which is encoded in the iaaM gene. In the second, the IAM is converted to IAA and ammonium, through an IAM hydrolase (IaaH), which is encoded by the iaaH gene. These genes have been described in bacteria such as *Agrobacterium tumefaciens*, *Pseudomonas savastanoi*, *Pseudomonas syringae*, *P. agglomerans*, *Rhizobium* sp. NGR234 and *Bradyrhizobium japonicum* (7, 27, 33, 34).

Plant growth promoter Bacteria

Plant-growth promoting bacteria (PGPB) are a group of beneficial plant bacteria (35). PGPBs participate in the growth and health of plants, eliminating damage caused by pathogenic microorganisms, synthesizing phytohormones, accelerating the availability and assimilation of soil nutrients through different mechanisms such as atmospheric nitrogen fixation, phosphorus solubilization and synthesis of siderophores (36, 37). In agriculture, PGPBs have been used as a sustainable alternative to the environment, since they have the capacity to improve soil quality and crop yields, reducing the negative impact of chemical fertilizers (38). PGPBs have been extensively studied in the last years and belong to the genera *Acetobacter*, *Acinetobacter*, *Alcaligenes*, *Arthrobacter*, *Azoarcus*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Beijerinckia*, *Burkholderia*, *Derxia*, *Enterobacter*, *Gluconacetobacter*, *Herbaspirillum*, *Klebsiella*, *Ochrobactrum*, *Pantoae*, *Pseudomonas* , *Rhodococcus*, *Serratia*, *Stenotrophomonas* and *Zoogloea* (36).

Bacteria that promote the growth of plants producing indole-3-acetic acid

The IAA produced by PGPB has a great impact on its plant growth promoting activity. Several bacteria of the taxonomic classes α-Proteobacteria, β-Proteobacteria, δ-Proteobacteria and Bacilli are PGPB producers of IAA; Some examples of PGPB are shown in the table. The phytostimulent effect of 16 strains of Bacillus on the growth of the plant Vigna radiata was studied. B. megateriumMiR-4, which corresponded to the largest producer of IAA, showed the greatest growth promoting effect, increasing shoot elongation and root number (39). Mutant bacteria of the ipdC gene lose plant growth promoter capacity. The root length of canola cuttings from seeds treated with P. putidaGR12-2 was 35 % longer than seed roots treated with the ipdC-mutant(22).

Growth promoting effect of plants of indole-3-acetic acid producing bacteria

Type of Bacterium	PGPB	Plant	Promoting effect
α-Proteobacteria	*Azospirillum brasilense* Sp245	*Arabidopsis thaliana*	Number of roots (42).
	Azospirillum brasilense SM	Sorgum	Root elongation and sprouts, number of roots (40).
	Acetobacter diazotrophicus PAl5	Cane sugar	Growth (Fresh and dry weight) (43).
β-Proteobacteria	*Burkholderia phytofirmans* PsJN	*Arabidopsis thaliana*	Number of roots and Growth (Fresh weight) (44).
	Burkholderia cepacia RRE25	*Oryza sativa*	Root elongation and sprouts, number of roots (45).
	Burkholderia xenovorans LB400	*Nicotiana tabacum*	Elongation and number of roots (41).
		Vitis vinifera	Rooting and number of roots [A].
δ-Proteobacteria	*Pseudomonas putida* GR12-2	Canola	Root elongation (22).
		Vigna radiata	Number of roots (22).
	Pantoea agglomerans PVM	*Nicotiana tabacum*	Rooting (46).
Bacilli	*Bacillus amyloliquefaciens* FZB42	*Zea mays*	Root elongation (47).
		Lemna minor	Growth (Fresh weight) (26).
	Paenibacillus polimyxa E681	*Cucumis sativus*	Growth (Fresh weight) (48).
	Bacillus megaterium MiR-4	*Vigna radiata*	Elongación de brotes y número de raíces (39).

The bacterium ipdC- by *Azospirillum brasilense* SM (SMIT56s10) decreased the growth-promoting effect on the number and length of roots of sorghum seeds (40). *Burkholderia xenovorans* LB400, a model bacterium for the degradation of various aromatic compounds, including polychlorinated biphenyls, has the ability to produce IAA via IPA. The LB400 strain promoted growth on plants such as *Nicotiana tabacum* and *Vitis vinifera*, thus increasing its metabolic versatility[A] (41).

CONCLUSIONS

- Indole-3-acetic acid auxin is a phytohormone of great importance for plant development, which can be synthesized through various metabolic vias.
- The IAA produced by PGPB plays a significant role in plant-microorganism interaction, contributing to the promotion of root and leaf growth of the plant.

[A] Vega-Celedón, P.; Canchignia, H.; González, M. y Seeger, M. ''Metabolism of indole-3-acetic acid in *Burkholderia xenovorans* LB400 and its effect on *Vitis vinifera* growth''. En: *XXI Congreso Latinoamericano de Microbiología*, Santos, Brasil, 2012.

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