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Microorganisms Stimulating Plant Growth for Sustainable Agriculture

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Abstract—The review deals with microorganisms capable of producing plant growth stimulators such as auxins, gibberellins, and cytokinins.

Keywords: Phytohormones, auxins, gibberellins, cytokinins, bacteria.

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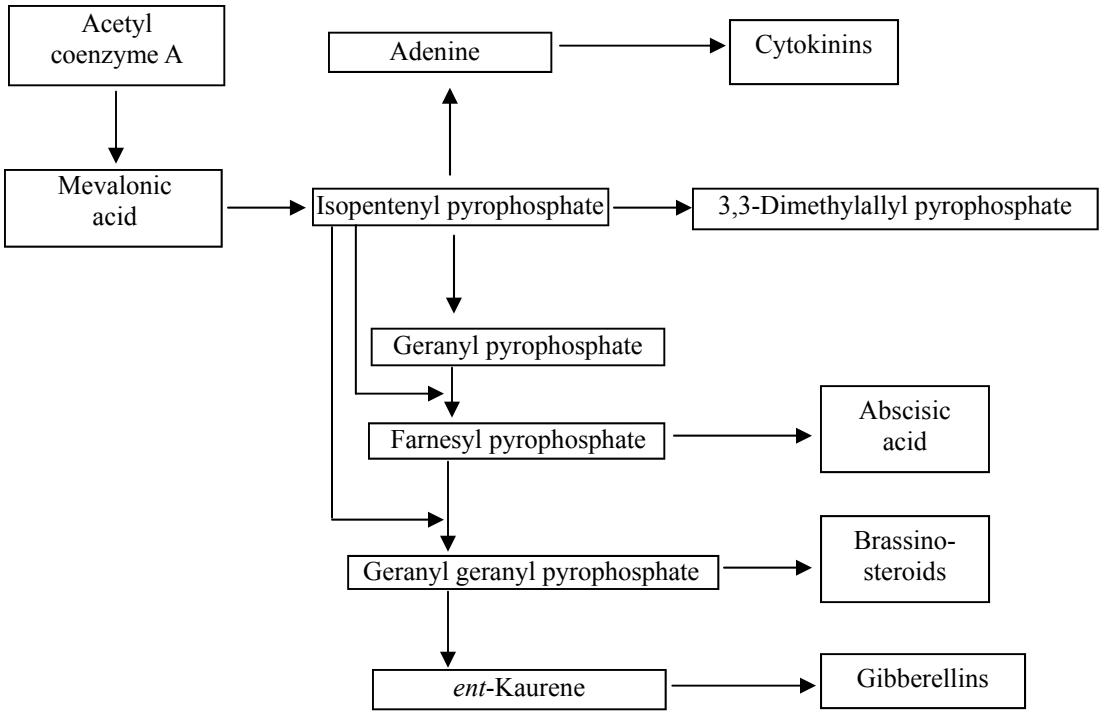
Soil plays the crucial role in the biosphere. As long as soil is sustainable, environmental safety is guaranteed. Loss or irreversible degradation of soil cover may be regarded as death of the ecosystem. The higher the anthropogenic load, the higher the risk of failure of mechanisms responsible for soil sustainability and the probability for soil transformation into a new state unsuitable for vital activity of biota and humans. Pollution of soils with heavy metals and petrochemicals, shortage of useful organic matter, and excess pesticides give rise to erosion and deflation. Microbiological approaches based on controlled activity of soil biocenoses are especially important for solving problems related to soil recovery. Soil microorganisms actively interact with plants, and they can both positively and negatively affect their growth and development.

It is known that plant cells produce phytohormones whose ratio determines all biological processes occurring in plants. Phytohormones are crucial not only for growth and morphogenesis but also for adaptive reactions to unfavorable environmental factors [1]. At present, five groups of phytohormones are distinguished: auxins, gibberellins, cytokinins, abscisic acid, and ethylene. This list is often supplemented by other substances such as brassinosteroids, jasmonic acid, salicylic acid, and some phenolic compounds [2]. Apart from plant hormones, signal molecules may include oligosaccharins (physiologically active oligosaccharides), lectins, and short peptides. The active concentration of these compounds is very low, about 10^{-12} to 10^{-15} M [3].

Most plant hormones are derived from organic acids, and several plant hormones can be formed from a single precursor. For example, mevalonic acid is the initial compound for the synthesis of four classes of phytohormones: stimulators gibberellins, cytokinins, and brassinosteroids and inhibitor abscisic acid (see figure). Variation in the production of one or another plant hormone, induced by internal or external factors, causes a plant species to change the character of growth in response.

Besides plants, many soil microorganisms (fungi, bacteria), specifically those colonizing plant roots (rhizosphere), are capable of improving plant growth via production of various metabolites, including growth stimulators. Metabolic growth stimulators affect not only the rate of plant growth but also such quailtative characteristics as the concentration of proteins, essential amino acids, and vitamins in plant biomass. Synthesis of plant hormones (auxins, gibberellins, and cytokinins) by these microorganisms is considered to be one of the main modes of interaction between the microflora and host plant [4].

The most widely occurring phytohormone produced by bacteria, is indole-3-acetic acid (IAA) which is classed with auxins. It is responsible for fission, stretching, and differentiation of plant cells and tissues. Among various effects of IAA in plants, the strongest effect is reflected in considerable acceleration of root formation [5]. The ability to produce IAA was found for photo- and chemoorganoheterotrophic bacteria



Phytohormone biosynthesis.

which comprise both symbiotic and non-symbiotic species [6]. For example, non-symbiotic *Azospirillum brasilense* [7] produces heteroauxin which stimulates plant growth and development. There are several ways of IAA biosynthesis by prokaryotes, and some bacterium species can produce heteroauxin in several ways simultaneously. All attempts to obtain *Azospirillum brasilense* mutants completely incapable of synthesizing IAA were unsuccessful. This indicates the existence of several ways of IAA biosynthesis by *Azospirillum brasilense* species. By adding tritium-labeled indole-3-acetamide and tryptophan to the nutrient medium it was shown that *A. brasilense* species can produce IAA in at least three ways. These are tryptophan-dependent indole-3-acetamide and indole-3-pyruvate (IPA) pathways and tryptophan-independent route. The IPA pathway of IAA biosynthesis was confirmed by the data of biochemical and genetic studies. This pathway dominates in *A. brasilense* cultivated in the presence of exogenous tryptophan. The first step in the IPA pathway is the conversion of tryptophan into indole-3-pyruvic acid, promoted by polyspecific aminotransferases. Indole-3-pyruvic acid is then converted into indol-3-acetaldehyde by the action of pyruvate decarboxylase, and indole-3-acetaldehyde is oxidized to IAA by the action of nonspecific aldehyde dehydrogenase.

Two aromatic amino acid aminotransferases were detected in *A. brasilense* strains Sp7, Sp245, UAPI4, and R07. However, genes encoding aminotransferases in *A. brasilense* were not identified. Ge at al. [7] discovered a novel gene, designated as *atrC*, and the products derived therefrom showed high similarity to aminotransferases of various bacteria. Mutagenesis and complementation studies demonstrated that just *atrC* is involved in the IAA production by *A. brasilense* [7].

Native *Azospirillum* species isolated from Iranian soils [8] were evaluated for the ability to affect the root growth of wheat. Wheat plants of 14 days old formed much longer roots and more root hairs and lateral roots after the inoculation with *Azospirillum* spp. The dry weight of the roots was 10.63 mg against 3.47 mg for control samples. *Azospirillum* sp. 118-I produced most IAA, 285.51 mg/L. The IAA production was shown to strongly depend on pH and the presence of vitamins, especially of pyridoxine and nicotinic acid.

Arthrobacter species isolated from the aquatic fern species *Azollu pinnata* and *Azolla filiculoides* produced IAA in the presence of tryptophan, while no IAA

production was detected in the absence of tryptophan [9]. The maximum IAA production by *Arthrobacter globiformis* (10.1 μg/mL in a nutrient medium containing 600 μg/mL of tryptophan) and *Arthrobacter nicotianae* (4.4 μg/mL in a nutrient medium containing 400 μg/mL tryptophan) was observed in the second day of the experiment, whereas *Arthrobacter crystallopoietes* produced a high level of IAA during 4-days incubation. Efficient IAA production (0.5–2.0 μg/mL) by the bacteria was also detected at lower tryptophan concentrations (25–50 μg/mL).

Some endotrophic associated bacteria isolated from the roots of Australian orchids (belonging to the genera *Pseudomonas*, *Bacillus*, and *Xanthomonas*) were found to produce IAA [10]. The auxin production was studied [10] in 42 bacterial strains isolated from the rhizoplane of greenhouse orchids: terrestrial *Calante vestita Lindl. var. rubrooculata* and epiphytic *Acampe papillosa* (*Lindl.*) *Lindl.* and *Dendrobium moschatum* (*Buch-Ham.*) *Swartz*. The bacterial cultures were grown by liquid-phase incubation in meat infusion broth and synthetic Czapek's medium with glucose. Such strains as *Sphingomonas* sp. 18, *Sphingomonas* sp. 42, *Microbacterium* sp. 23, *Rhizobium* sp. 5, *Pseudomonas* sp. 62, *Pseudomonas* sp. 4, and *Micrococcus luteus* produced 10–28 μg/mL of IAA, while the concentration of IAA in the culture liquid of *Rhodococcus* sp. 16, *Rhodococcus* sp. 28, *Rhodococcus* sp. 21, *Microbacterium* sp. 25, *Micrococcus* sp. 8, and others was about 1 μg/ml. The maximum IAA concentration in the culture liquid was obtained in the early and late stationary growth phases. In the absence of tryptophan, the level of IAA production in Czapek's medium (0.3–6.6 μg/mL) was lower than in meat infusion broth (4.8–28.1 μg/mL). The highest stimulating effect of tryptophan was observed at a concentration of 200 μg/mL. Under these conditions, bacteria isolated from the roots of *Dendrobium moschatum* (*Sphingo-monas* sp. 18, *Microbacterium* sp. 23, *Mycobacterium* sp. 1, *Bacillus* sp. 3, and *Rhizobium* sp. 5) produced 50.2, 53.1, 92.9, 37.6, and 60.4 μg/ml of IAA, respectively, while those isolated from the roots of *Asatre papillosa* (*Sphingomonas* sp. 42, *Rhodococcus* sp. 37, *Cellulomonas* sp. 23, *Pseudomonas* sp. 24, and *Micrococcus luteus*), produced 69.4, 49.6, 53.9, 31.0, and 39.2 μg/ml of IAA, respectively. On the average, addition of 200 μg/ml of tryptophan to the nutrient medium increased the amount of auxins excreted by the bacteria by a factor of 30 (*Sphingomonas* sp. 18, *Mycobacterium* sp. 1, *Rhizobium* sp. 5, *Cellulomonas* sp. 23, *Micrococcus luteus*). The addition of tryptophan to the nutrient medium stimulated production of auxins by *Pseudomonas* sp. 24 to the greatest extent (by a factor of 170), and the lowest effect (by factors of 3 and 8) was observed for two species of the genus *Bacillus.*

Methylotrophic bacteria, as well as representatives of the genera *Arthrobacter* and *Pseudomonas* produced 5–15, 20–25, and 90–120 μg/mL of IAA in the presence of 200–500 μg/mL of tryptophan [11]. Aerobic methylotrophic bacteria widely occur in nature and are closely associated with plants. This is determined, on the one hand, by secretion of methanol (as carbon source for growth of methylotrophs) by plant cells, and on the other, by the ability of methylotrophs to produce auxins. Experiments *in vitro* revealed stimulation of root formation in explants of various plants infected with methylotrophic bacteria. These findings suggested the possibility for auxin production by the bacteria. It was also found that various methylotrophic and methanotrophic bacteria grown in methane-, methanol-, or methylamine-containing media in the presence of 5 mmol/L of tryptophan produce indole compounds, in particular IAA. The amount of indole compounds excreted by different methylotrophs ranged from 3 to 100 μg/mL. The auxin production was enhanced by addition of tryptophan to the nutrient medium and was inhibited by ammonium ions. Apart from IAA, *Paracoccus kondratieva* and *Methylovorus mays* released β-(indol-3-yl)lactic acid which was detected by TLC and HPLC. Methylotrophic bacteria that assimilate formaldehyde via the serine pathway (*Methylobacterium mesophilicum* and *Aminobacter aminovorans*) also produced indole-3-pyruvic acid and indole-3-acetamide. It was revealed that the IAA biosynthesis pathway in *M. mesophilicum*, *M. mays*, *A. aminovorans*, and *P. kondratievae* involves indole-3-pyruvic acid. Thus it was demonstrated for the first time that aerobic methylotrophic bacteria are capable of producing phytohormones (auxins), which indicates their symbiotic relation with plants.

The ability of rhizosphere pseudomonades to produce IAA has been well documented [12–14]. However, most plant growth-promoting pseudomonade strains produce IAA in very small amounts (3–5 μg/mL), whereas growth-inhibiting species produce up to 20 μg/mL of IAA. Studies on the synthesis of IAA by plant growth-promoting rhizobacteria (PGPR) of the genus *Pseudomonas* demonstrated the pos-

sibility for obtaining genetically modified PGPR *Pseudomonas* strains with enhanced capability of producing IAA [12]. Inoculation of PGPR *Pseudomonas* with some naphthalene biodegradation plasmids also favored increase of the IAA production level in rhizosphere pseudomonades due to the presence in these plasmids of a gene responsible for the synthesis of naphthalene dioxygenase (the first enzyme in the naphthalene oxidation pathway) which is involved in the biosynthesis of IAA. It should be noted that, apart from IAA, *Pseudomonas* species can produce other plant growth regulators, in particular gibberellin-like compounds [14].

According to Sequeira et al. [15], the concentration of IAA in tobacco plants infected with *Pseudomonas solanacearum* was higher than in the healthy plants, which also indicates IAA production by bacteria of the genus *Pseudomonas*.

Phytohormones were detected among *Streptomyces* metabolites. Burtseva et al. [16] studied the effect of *Streptomyces levoris 22* exometabolites on the root formation in grape stem cuttings characterized by different regenerative abilities. The ability of this bacterial strain to produce heteroauxins was revealed previously by the same research team. The studies were carried out under controlled conditions with industrial and table grape varieties resistant to phylloxera. The root formation by stem cuttings was found to be determined by specific varietal features and physiological activity of tissues. Streptomycete exometabolites favored increase in the number of roots, their length, and rootstock growth. The effect of *Streptomyces levoris* exometabolites on the regeneration of stem cuttings was observed in grape varieties with both high (Moldova) and moderate (Viorika) rhizogenic activity. Thus, it was demonstrated that Streptomycete exometabolites are promising for practical use to promote root formation in grape stem cuttings characterized by different rhizogenic activities.

Tret'yakova et al. [17] reported on the effect of *p. Streptomyces* and *p. Trihoderma* metabolites (including auxins) on embryogenic calluses and somatic embryos of coniferous species. Stimulation effect of microbial metabolites on the formation, growth, and viability of callus cultures of Dahurian and Siberian larches, Siberian pine, and Siberian dwarf pine was established, the effect being species-specific.

Inoculation of kidney bean with *Bradyrhizobium* species resulted in elongation of the pod-bearing node, whereas inoculation of rice with *Rhizobium* species led to elongation of roots and increased productivity; these findings indicated production of plant hormones by the above bacterial genera [18]. Yagi et al. [19] isolated 11 low-IAA-producing mutants of *Bradyrhizobium elkanii* by Tn5 mutagenesis. The amount of IAA produced by each mutant was 2.2–13.6% of that of the wild strain.

Cyanobacteria are promising as ecologically friendly biofertilisers [20]. Their role as source of organic matter and phytohormones is especially important in biocenoses developing in extreme environment where higher plants are not viable at all or their contribution to the development of biocenosis is considerably reduced. The isolation and study of active nitrogen-fixing and phytohormone-producing strains of cyanobacteria, capable of stimulating plant growth in saline soils, attract much interest. Kadyrova et al. [21] selected the following strains of salt-tolerant filamentous and single-celled cyanobacteria: *Nostoc calcicola*, *Nostoc pruniforme*, and *Gloeothece rupestris* and examined the effect of the corresponding culture liquids on the germination capacity of cotton seeds *in vitro*. It was found that the culture liquids at a dilution of 1 : 1000 stimulated germination rate and capacity and seed vigor by 40–50%, while inhibitory effect was observed at higher concentrations (dilution 1 : 10). Analogous effects were produced by IAA solutions. The production of IAA by cyanobacteria was evaluated at several tryptophan concentrations, 1, 3, and 5 mg/mL. The concentration of IAA was measured after incubation for 3 and 7 days in the presence of tryptophan. *Nostoc calcicola, Gloeothece rupestris*, and *Anabaena variabilis* turned out to be the most efficient IAA producers. These strains produced 10.2, 8.2, and 7.4 mg/L of IAA, respectively, after incubation for 3 days in tryptophan-free medium and 20.5, 15.5, and 13.6 mg/L of IAA after incubation for 7 days. The IAA level produced by the most active *Nostoc calcicola* strain after 7-days incubation was 50.45, 97.5, and 210 mg/L at a tryptophan concentration of 1, 3, and 5 mg/mL, respectively.

Garipova [22] described two strains of legume-associated nodule bacteria (sp. 12 and sp. 101), which were selected by their nitrogenase activity and virulence to pea plants; they ensured a 1.5-fold increase in productivity as compared to inoculation with a standard strain and to control samples in field experiments. In one case, the observed increase was achieved due to enhanced nodulation, and in the

second, due to production of growth-stimulating compounds, mostly of auxins. The presence of associated bacteria in the rhizosphere considerably increased the plant weight (by 33–73%). These findings indicated an important role of nodule bacteria as potential biocontrol agents and producers of plant growth stimulators.

Flavobacterium sp. OCM-1 isolated from oil-polluted soil was found to degrade carbazole and produce IAA, as shown by thin-layer chromatography and spectral methods [23]. From 250 mg of carbazole 1.5 mg of IAA is obtained.

According to El Sorra et al. [24], rhizobacterium *Bacillus amyloliquefaciens* FZB42 produces phytohormone-like acting compounds. Indole-3-acetic acid (IAA) was detected by HPLC and GC/MS in the culture filtrates of FZB42. A high level of IAA production (29.3 ng/mL) was observed in a culture medium containing no tryptophan, whereas addition of the latter to a concentration of 0.1 to 1.0 mM raised the yield of IAA to 51–54 ng/mL, and the concentration of IAA reached 161 ng/mL in the presence of 5 mM of tryptophan. The ability to generate IAA was also found for the gram-positive phytopathogenic bacterium *Rhodococcus fascians* [24].

Karadeniz et al. [25] found that *Proteus mirabilis*, *Proteus vulgaris*, *Bacillus megaterium*, *Bacillus cereus*, *Klebsiella pneumoniae*, and *Escherichia coli* produce IAA, gibberellic acid (GA), zeatin, and abscisic acid (ABA) in both free and bound forms. For example, the highest concentration of IAA in the *Klebsiella pneumoniae* culture liquid, 0.5068 mg/L, was detected after 6-h incubation. *Proteus mirabilis* showed the highest efficiency: after incubation for 6 h, the cultural liquid contained 0.7052 mg/L of GA, 0.0229 mg/L of zeatin, and 0.0420 mg/L of ABA.

Gibberellins (GA) are produced by higher plants, fungi, and bacteria. It is known that 128 plant species produce 136 GAs, 28 GAs are synthesized by seven fungi species, and only four gibberellins (GA_1, GA_3, GA_4, and GA_{20}) are generated by 7 bacterial species. In keeping with published data, representatives of epiphytic and rhizosphere bacteria belonging to the genera *Azotobacter*, *Arthrobacter*, *Azospirillum*, *Pseudomonas*, *Bacillus*, *Acinetobacter*, *Flavobacterium*, *Micrococcus*, *Agrobacterium*, *Clostridium*, *Rhizobium*, and *Xanthomonas* are capable of producing gibberellins [18].

Joo et al. [18] isolated and identified a new strain of gibberellin-producing bacteria, *Burkholderia* sp. (KSTS 11096BP). Analysis of the culture filtrate showed the presence of several gibberellins, both physiologically active (GA_1, 0.23 ng/100 mL; GA_3, 5.11 ng/100 mL; GA_4, 2.65 ng/100 mL) and inactive (GA_9, GA_{12}, GA_{15}, GA_{20}, GA_{24}). The bacteria also dissolved tricalcium phosphate and reduced pH during the incubation.

Gibberellin production by *Bacillus pumilus* and *Bacillus licheniformis* and production of auxin-like compounds by *Bacillus subtilis* and *Bacillus amyloliquefaciens* were detected by GC/MS [24]. *Acetobacter diazotrophicus* and *Herbaspirillum seropedicae* were also found to produce gibberellins [26]. The effects of inoculation with *Acetobacter diazotrophicus* and of applications of GA_3 at several doses were assessed in shoots of *Sorghum bicolor*. Both *A. diazotrophicus* and GA_3 were effective in promoting total carbohydrate accumulation, but none of these techniques increased the sucrose level. By contrast, the concentrations of fructose and glucose were significantly raised in both cases [26]. The dwarf phenotype in *A. glutinosa* was effectively reversed by applications of extracts from the medium incubated with both bacteria and also by exogenous GA_3. GC/MS analysis of the extracts showed the presence of GA_1, GA_3, GA_4, and GA_{20}. Probanza et al. [27] also reported that inoculation with *Bacillus licheniformis* and *B. pumilus* enhanced growth of *Pinus pinea* plants, presumably due to gibberellin production by the bacteria.

Fett at al. [28] detected 0.03–6.37 μg/mL of IAA in the *Xanthomonas campestris* culture medium containing 0.05% of tryptophan. Costacurta et al. [29] found 11.6–55.3 μg of IAA in 400 ml of culture medium without addition of tryptophan in the late exponential phase of bacterial growth of different strains of *Xanthomonas axonopodis* which is pathogenic to citrus. In another study [30], obligate and facultative methylotrophic bacteria produced auxins, in particular IAA, in amounts of 3–100 μg/mL. Pedraza et al. [31] studied production of IAA by nitrogen-fixing bacteria and found that *Azospirillum* strains produced the highest concentrations of IAA (16.5–38 μg IAA/mg protein), whereas *Gluconaceto-bacter* and *Pseudomonas stutzeri* strains produced lower concentrations of IAA (1 to 2.9 μg/mg protein) in a culture medium supplemented with tryptophan. Taller and Wong [32] determined cytokinins as equivalent to 0.75 μg/L of kinetin in *Azospirillum vinelandii* culture medium. Barea and Brown [33] detected 20 μg/L of cytokinin equivalent in the culture liquid of *Azotobacter paspali*

and 50 μg/L for *Azospirillum vinelandii*. Studies on *Azotobacter chroococcum* [34] showed that this bacterial strain produces IAA, GA_3, and cytokinins in a nitrogen-free culture medium supplemented with maize root exudates and 0.5% of glucose. Plant growth hormones GA_3, GA_1, and *iso*-GA_3 were detected in the *Azospirillum lipoferum* culture medium [35]. Bottini et al. [36] estimated the amount of GA_1 and GA_3 produced by *Azospirillum lipoferum* at 20–40 pg/mL. It was also found that *Agrobacterium tumefaciens*, *Pseudomonas savastanoi*, *Bradyrhizobium japonicum* 61A68, and *Corynebacterium fascians* produce cytokinins and that *Proteus mirabilis*, *Proteus vulgaris*, *Bacillus megaterium*, *Bacillus cereus*, *Klebsiella pneumoniae*, and *Escherichia coli* produce IAA, GA_3, zeatin, and ABA [25].

A cytokinin hyperproducer strain, *Bacillus subtilis* IB-22, was revealed among aerobic spore-forming bacteria of the genus *Bacillus*. The culture liquid of IB-22 contained a novel form of biologically active bound cytokinins, which was identified as a complex of hormones with polysaccharide [36].

The available data on bacterial strains producing phytohormones are summarized in table.

Apart from bacteria, various fungi species are capable of producing phytohormones. Many saprophytic and phytopatogenic fungi species excrete considerable amounts of auxins, gibberellins, cytokinins, and vitamins during their vital activity or under certain incubation conditions. For example, *Phanerochaete chrysosporium* ME446 produces IAA and ABA. The

Phytohormone-producing microorganisms

Microorganism	Auxins	Gibberellins	Cytokinins
Acetobacter sp.	+		
Acetobacter diazotrophicus		+	
Achromobacter sp.	+		
Acinetobacter sp.	+	+	
Agrobacteriit sp.	+	+	
Agrobacterium tumefaciens			+
Alcaligenes sp.	+		
Aminobacter sp.	+		
Aminobacter aminovorans	+		
Anabaena variabilis	+		
Arthrobacter sp.	+	+	
Arthrobacter globiformis	+		
Azospirillum sp.	+	+	
Azospirillum brasilense	+		
Azospirillum brasilense R07	+		
Azospirillum brasilense sp. 245	+		
Azospirillum brasilense sp. 7	+		
Azospirillum brasilense UAPI4	+		
Azospirillum lipoferum		+	
Azospirillum sp. 118-I	+		
Azospirillum vinelandii			+

Table. (Contd.)

Microorganism	Auxins	Gibberellins	Cytokinins
Azotobacter sp.	+	+	
Azotobacter chroococcum	+	+	+
Azotobacter paspali			+
Bacillus sp.	+	+	
Bacillus amyloliquefaciens	+		
Bacillus amyloliquefaciens FZB42	+		
Bacillus cereus	+	+	+
Bacillus licheniformis		+	
Bacillus megaterium	+	+	+
Bacillus pumilus		+	
Bacillus sp. 3	+		
Bacillus subtilis	+		
Bacillus subtilis IB-22			+
Bradyrhizobium sp.	+		
Bradyrhizobium elkanii	+		
Bradyrhizobium japonicum 61A68	+		+
Burkholderia sp. (KSTS 11096BP)		+	
Corynebacterium sp.	+		
Corynebacterium fascians	+		+
Cellulomonas sp. 23	+		
Clostridium sp.		+	
Escherichia coli	+	+	+
Flavobacterium sp.	+	+	
Flavobacterium sp. OCM-1	+		
Gloeothece rupestris	+		
Gluconacetobacter sp.	+		
Herbaspirillum seropedicae	+	+	
Klebsiella sp.	+		
Klebsiella pneumoniae	+	+	+
Methylobacterium sp.	+		
Methylobacterium mesophilicum	+		
Methylovorus sp.	+		
Methylovorus mays	+		
Microbacterium sp. 23	+		

Table. (Contd.)

Microorganism	Auxins	Gibberellins	Cytokinins
Microbacterium sp. 25	+		
Micrococcus sp.	+	+	
Micrococcus luteus	+		
Micrococcus sp. 8	+		
My-cobacterium sp. 1	+		
Nostoc calcicola	+		
Nostoc pruniforme	+		
Paracoccus sp.	+		
Paracoccus kondratievae	+		
Phaseolus lunatus	+		
Proteus mirabilis	+	+	+
Proteus vulgaris	+	+	+
Pseudomonas sp.	+	+	
Pseudomonas solanacearum	+		
Pseudomonas sp. 24	+		
Pseudomonas sp. 62	+		
Pseudomonas savastanoi			+
Pseudomonas stutzeri	+		
Rhizobium sp.	+	+	
Rhizobium sp. 5	+		
Rhodococcus sp.	+		
Rhodococcus fascians	+		
Rhodococcus sp. 16	+		
Rhodococcus sp. 21	+		
Rhodococcus sp. 28	+		
Rhodococcus sp. 37	+		
Sphingomonas sp. 18	+		
Sphingomonas sp. 42	+		
Streptomyces sp.	+		
Streptomyces levoris 22	+		
Xanthomonas sp.	+	+	
Xanthomonas axonopodis	+		

maximum auxin level was detected on the 18th day of incubation in free and immobilized cells (55.91 and 76.07 μg/mL, respectively). The highest concentration of ABA on the 12th day was 6.87 and 10.69 μg/mL, respectively. It was concluded that immobilized cells of *Phanerochaete chrysosporium* ME446 produce larger amounts of auxin and ABA than do the free cells [37].

Chung and Tzeng [38] reported that the fungus *Ustilago esculenta* prevents inflorescence and seed production in aquatic grass *Zizania latifolia* due to IAA production. The maximum amount of IAA (1.0 μg/mL) was obtained after incubation for 8 days. The IAA production was enhanced by addition of tryptophan, and the optimal temperature ranged from 20 to 25°C. However, variable temperature conditions considerably reduced IAA production by the fungus, indicating that a constant temperature is an important factor affecting the synthesis of IAA. In addition to tryptophan, *U. esculenta* is capable of transforming indole-3-acetamide, indole-3-pyruvate, and indole-3-lactic acid into IAA. The corn smut pathogen *Ustilago maydis* [38] produced IAA upon addition of tryptophan, the maximum amount of IAA (~1.2 μg/mL) being detected on the third day of incubation. The amount of IAA produced by the sugarcane smut pathogen *Ustilago scitaminea* under analogous conditions was lower (0.53 μg/mL).

An IAA-producing strain, *Kitasatospora* sp., isolated from soil was encapsulated in calcium alginate beads for soil applications [39]. Samples were examined by optical and scanning electron microscopy. The bead surface was found to be colonized by the fungus; initially, growth of hyphae was observed, and after 7 days, sporulation. Immobilized cells produced a higher IAA concentration (2.7 μg/mL) as compared to the free cells (1.5 μg/mL). Analogous results were obtained when free and entrapped cells were inoculated in a sterile soil-simulating medium. *Kitasatospora* sp. demonstrated a good tolerance to environmental conditions, such as temperature, salinity, heavy metals, and pH.

It is known that gibberellins were isolated for the first time from *Gibberella fujikuroi* (the anamorph belongs to the genus *Fusarium*). Nava Saucedo et al. [40] studied continuous production of gibberellic acid by *Gibberella fujikuroi* in a fixed-bed reactor. The results showed that the yield of GA_3 from immobilized mycelium was 0.408 mg per gram of biomass per day, and from the free mycelium, 0.384 mg per gram of biomass per day. It was concluded that the use of immobilized *Gibberella fujikuroi* mycelium is more profitable for the synthesis of gibberellic acid. According to the data of Kumar and Lonsane [41], *Gibberella fujikuroi* P-3 produced 0.58–0.66 mg L^{-1} h^{-1} of GA_3 in a similar bioreactor.

CONCLUSIONS

In summary, problems related to microorganisms producing plant growth regulators, in particular auxins, gibberellins, and cytokinins, are important and practical. However, no systematic studies have been performed on the ability of microorganisms to produce phytohormones. Available data often pertain to particular species or strains, while numerous species have not been studied at all as plant growth regulator promoters.

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