REVIEW ARTICLE

The Effect of Auxin and Auxin-Producing Bacteria on the Growth, Essential Oil Yield, and Composition in Medicinal and Aromatic Plants

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Abstract

Aromatic plants had been used since ancient times for their preservative and medicinal properties, and to impart aroma and flavor to food. Also their secondary metabolites are economically important as drugs, flavor and fragrances, pharmaceuticals, agrochemicals, dye, and pigments, pesticides, cosmetics, food additives, other industrially biochemical, and also play a major role in the adaptation of plants to their environment. Indole acetıc acid-producing rhizobacteria inoculations increase in stomatal density and level of secondary metabolite and have a synergistic effect on monoterpene biosynthesis. Bacterial inoculation significantly affected and increased the chemical composition of essential oil, citronellol, and geraniol content in rose-scented geranium; essential oil composition and total phenolic content in marigold; density, number, and size of glandular trichomes in sweet wormwood and peppermint essential oil components such as geranyl acetate, limonene, and β–pinene in coriander; oil yield and content in calendula; yield of the herb in hyssop; oxygenated compounds, essential oil content and yield, anethol and changing the chemical composition in fennel; growth, number of glandular trichomes and essential oil yield, root branching and length, and total amount of essential oil, production of monoterpenes such as pulegone, menthol, menthone, menthofuran, and terpineol content, biosynthesis of secondary metabolites in peppermint; growth and essential oil yield in marjoram; glandular hair abundance, essential oil yield, and monoterpene biosynthesis in basil; phellandrene, limonene, borneol, and campor in rosemary; carvacrol, thymol, linalool, and borneol in oregano; and α-thujene, α-pinene, α-terpinene, p-simen, β–pinene, and γ-terpinene contents and essential oil yield in summer savory. Inoculation with IAA-producing bacteria medicinal roots increased the valerenic acid in valerian, essential oil and quality in vetiver, curcumin content in turmeric alkaloid and ginsenoside content in ginseng, and inulin content in Jerusalem artichoke.

Introduction

Plant hormones are usually divided into five main groups namely; auxins, cytokinins, gibberellins, abscisic acid, and ethylene. In addition, the current discovered phytohormones belong to the group of strigolactones, brassinosteroids, jasmonic acid, salicylic acid, polyamines, and nitric oxide hormones [1–3]. Auxins, cytokinins, gibberellic acid, abcisic acid, and ethylene are the names of five main classes of plant hormones and they are known as the signal molecules required in many plant development processes [4–6], however, there are many prominent evidences are in hands that

other compounds also regulate growth in plants. Auxins are the most important group of plant hormones that affect plant growth and development either alone or in combination with other plant hormones [7]. Moreover, the levels of auxin are affected by plant hormones namely; cytokines, ethylene, gibberellins, jasmonates, and brassinosteroids [6, 8–10].

Auxins are divided into two basic groups such as naturally occurring and synthetic auxin analogs. There are five naturally occurring auxins in plants include indole-3-acetic acid (IAA), 4-chloroindole-3-acetic acid (4-Cl-IAA), phenyl acetic acid (PAA), indole-3-butyric acid (IBA), and indole-3-propionic acid (IPA) [11, 12]. In addition to endogenous auxins, many synthetic compounds having auxinic activity, called synthetic auxin, that have been synthesized and developed. Some of the commonly known synthetic auxins are: 2,4-dichlorophenoxyacetic acid (2,4-D), α-naphthalene acetic acid (α-NAA), 2-methoxy-3,6-dichlorobenzoic acid (dicamba), 4-amino-3,5,6-trichloropicolinic acid (tordon or picloram), 2,4,5-trichlorophenoxyacetic acid (2,4,5-T),

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and so on [13, 14]. Although many natural and synthetic compounds show auxin-like activity in bioassays, IAA is the best known and physiologically the most active natural auxin in the plant and is recognized as the key auxin in most plants. Indole-3-acetic acid, the major natural auxin found in plants is a signaling substance involved in almost every plant developmental process and plays a key role in the early stages of adventitious rooting [12, 15].

Indole-3-acetic acid (IAA) is one of the best-characterized auxin and the essential plant hormones that has the capacity to control plant growth. Many of bacteria have plant growth-promoting or phytopathogenic characteristics that can synthesize IAA. Indole-3-pyruvic acid, indole-3-acetamide, and indole-3-acetonitrile are the three basic ways for IAA synthesis [16]. For instance, it has been shown that the most important auxin, produced by the *Azospirillum* is the IAA [17, 18], while in some studies [19], indole-3-butyric acid (IBA) can be produced at a high rate and converted to IAA. *Azospirillum* can produce IAA at all stages of development [20]. It has been reported by Duca et al. [21] that the IBA is an important source and reserve for the IAA in *Azospirillum* strains, *Azospirillum* sp. can produce IAA in four different ways, three of them would be tryptophan-dependent indole-3-pyruvic acid, indole-3-acetamide and tryptamine, and the other as tryptophan-free way. The levels of IAA increase due to fluctuations in environmental factors, nutrient deficiencies, especially the limitation of nitrogen, carbon, and phosphorus [20]. The IAA is the most common endogenous auxin which plays a role in root development and elongation, and it is a common product of L-tryptophan metabolism by several microorganisms including plant growth-promoting bacteria (PGPB) [21–25]. IBA is an endogenous compound that appears to regulate both lateral and adventitious root formation [26]. Auxin production is considered as an important factor in the ability of rhizospheric bacteria to promote plant growth directly [27–29]. A significant proportion of the bacteria isolated from the rhizosphere and endosphere produced IAA, and the rhizosphere bacteria produced more indolic compounds than the other parts of rhizosphere found in soil [30–34]. The synthesis of indolic compounds in bacteria depends on the precursors in root secretions. Among the different root secretions, L-tryptophan has been identified as the main precursor of the synthesis of bacterial indolic compounds [35]. Microbial auxin production is not only responsible for strengthening the relationship between plant and microorganisms, but also is an important factor that positively promotes plant growth and development. In this way, bacterial auxin production potential is considered effective in reducing the hazardous effects of chemical fertilizers on the ecosystem and can be used to improve higher yields and growth [36]. Auxin production by PGPB activates biosynthetic signaling pathways [37]. It is thought that microbial auxin production by PGPB changes the auxin level and affects all physiological processes due to the critical effects of the level of auxins on plant growth and thus improving plant growth and yield [38].

Organic nitrogen sources stimulate IAA production in a better way than that of inorganic nitrogen sources [16, 20, 39]. The bacterial effect in the plant rhizosphere is largely related to the production of auxin phytohormone and indolic compounds such as IAA produced by many bacterial species play an important physiological role in rhizobacteria–plant interactions [40–42]. Jasim et al. [43] reported that, IAA synthesis by bacteria may have various regulatory effects in plant–bacterial interactions and significant effect on plant growth promotion. IAA-producing isolates can enhance and improve the compatibility of the plant–microorganism interaction [44, 45], and bacterial IAA stimulates the development of the root system of the host plant and allows more bacteria to be deployed in the rhizosphere by increasing root secretions [45, 46]. As in the defense mechanism, IAA is involved in almost all stages of growth and development of the plant. Bacterial IAA loosens plant cell walls, resulting in an increase in the amount of root exudations that provides additional nutrients to support the growth of rhizosphere bacteria [47, 48]. IAA stimulates excessive production of capillary roots hairs and lateral roots in the plant and promotes the release of saccharides from plant cell walls during the elongation process [49]. The IAA plant produced by the bacteria affects the plant physiological processes by changing the auxin pool. Moreover, bacterial IAA affects the morphology and development of root; then the root increases its surface area, volume, and length and it also allows the plant to reach the nutrients more easily in the soil. Consequently, PGPB indirectly promotes plant growth by increasing nutrient uptake [50] and also modify root functioning, improve plant nutrition, and influence the physiology of the whole plant [51, 52]. Inoculation with PGPB modulate root architecture due to increased IAA level, which allows plants to uptake more nutrients under salinity and drought stress [51–55].

Indole-3-acetic acid, an auxin compound, is produced by bacteria in different biosynthetic ways [4, 40]. Several microorganisms living in the plant rhizosphere can synthesize auxin as the secondary metabolite due to the rich substrates leaking from the roots as compared to the non-rhizosphere soil and it releases the auxin free in the environment [22, 56, 57]. A part of IAA secreted by the bacteria is taken up by plant cells and it induces cell division in the plant along with the plant's endogenous IAA content [58]. 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity can be increased by microbial auxin production because auxin stimulates the biosynthesis of ACC synthase enzyme in the plant which results an increase in ACC expression [59, 60]. As a result of the interaction between IAA and ACC, ACC deaminase is that

by lowering plant ethylene levels, facilitates the stimulation of plant growth by IAA [17]. IAA secreted by bacteria can increase root growth by stimulating cell division or cell elongation in plant, furthermore, it can produce ACC deaminase indirectly [61]. In general, the bacterial IAA and ACC deaminase can increase the root surface area and length making the plant easier to access to nutrients and water in the soil [62]. On the other hand, PGPB, which simultaneously contains IAA and ACC deaminase, can lead to a better growth of plants as compared to IAA or ACC producer bacteria alone [63, 64].

Auxin production potential is not only limited to rhizospheric PGPBs, but also endophytic bacteria and plant growth-promoting fungi can produce auxins. Bacteria have been reported to produce cytokines and other plant hormones i.e., gibberellin, but the vast majority of plant hormone-producing bacteria can also produce IAA [65, 66]. An important part of rhizospheric bacteria can produce IAA. *Erwinia herbicola*, *Agrobacterium tumefaciens*, *Agrobacterium rhizogenes*, and *Pseudomonas syringae* like pathogenic bacteria and *Azotobacter*, *Pseudomonas*, *Azospirillum*, *Bacillus*, *Paenibacillus*, *Burkholderia*, *Enterobacter*, *Aeromonas*, *Alcaligenes*, *Pantoea*, *Streptomyces*, and *Rhizobium* like plant growth-promoting species can produce IAA [16, 23, 37, 38, 67–73]. Many bacteria species including soil, epiphytic, endophytic, marine, methylotrophs, and cyanobacteria have the ability to synthesize IAA [42, 74–76]. Plants provide suitable shelter and nutrient containing secretions to the millions of IAA-producing and mutually beneficial bacterial partners of these genera. Bacterial IAA increases the number and length of side and primary roots in the ideal concentration range by stimulating the formation of fibrous root, however, bacterial IAA inhibits primary root growth at high concentrations [49].

Among the various mechanisms involved in plant growth enhancement by PGPR is microbial auxin production, which has been reported to play major role in growth improvement of plants by PGPRs. The majority of bacteria cultured from plants are IAA producers, a fundamental substance in the plant life cycle. Auxins action and interaction regulate most of the physiological activities and growth in plants, and the production of indole acetic acid (IAA) is a vital feature of rhizobacteria that stimulate and facilitate plant growth and development [77]. In the production of many medicinal and aromatic plant species consumed without further processing, it is of great importance to avoid the use of chemical inputs and to develop growth-promoting strategies involving phytohormone-producing PGPR and bio-fertilizers. Therefore, this review focuses on the effect of effects of auxins, external IAA applications and IAA-producing bacterial inoculations on growth, yield, and essential oil content and components of medicinal and aromatic herbs, seeds, roots, tubers, bulbs and rhizomes.

Effects of Auxins on Plants

Generally, IAA hormone in plants plays an important role in cell division, proliferation, and differentiation, vascular tissue alteration, responses to light and gravity, general root and shoot architecture, seed and tuber germination, organ differentiation, peak predominance, ethylene synthesis, vegetative growth processes, fruit development and aging [16, 49, 78], initiation of lateral and floral organ and organogenesis [79], initiation of rooting, foliation and flowering [80], formation of lateral and adventitious roots [81, 82], and increasing the growth of cambium and size of xylem cells [83]. Auxin in particular is central to the establishment and maintenance of a root meristem. IAA also affects fluorescence and photosynthesis, pigment formation, biosynthesis of various metabolites, and resistance to stress conditions [52, 78]. Auxin is also effective in the growth and seed development of oilseed crops, subsequently increasing the production of oils from seeds. Among different plant hormones that play a role in regulating reproductive plant growth, auxins trigger flower and fruit development programs that are closely related to flower and fruit development [84]. Villacorta et al. [85] reported that IAA is the most abundant plant hormone and is associated with both vegetative and reproductive development in hop (*Humulus lupulus*) plants. Furthermore, previous reports suggest that the mechanism involved in indole-mediated signaling in plants leading to significant plant growth promotion [86].

The cells in the vicinity of the developing leaves often consume auxins, thus limiting the formation of new leaves that are very close to each other. An important part of auxins help the young leaves and fruits to remain intact, whereas, a decrease in auxin level leads to separation in the branch of the petiole or the stem of the fruit and causes the leaves and fruits to fall on ground. Studies show that inadequate IAA-producing plants lost their ability to avoid shade and showed a stunted growth as compared to normal plants [87]. In addition, the use of reactive oxygen species in combination with auxin may provide plants with a mechanism to optimize plant performance during stress [8]. It has been determined that IAA applications stimulate the number of branches, length of stem, number of nodes per plant, callus development, and formation of root and stem in *Melissa officinalis* [88].

The most common of hormones are auxins and IAA is one of the most active physiological auxins in plants. Auxins stimulate the root formation and initiation of lateral roots. Low concentrations of exogenous IAA can stimulate primary root elongation, whereas high IAA levels enhance formation of lateral roots and root hairs [61, 89]. However, auxins delay root development at higher concentrations

but stimulate the growth of root at certain optimal levels [9, 36, 90]. The inhibitory effect of high auxin concentrations on the plant roots is the result of an increase in the stimulation of ethylene synthesis by increasing the auxin level of ACC synthesis which is the precursory substance of ethylene and the inhibition of root growth by auxins has been found to be reversed by the application of inhibitors of ethylene synthesis [10, 36]. Ethylene is necessary in the process of seed germination but high concentrations of ethylene can lead to the prevention of root growth after germination. On the other hand, it has been found that PGPBs inhibit the activity of ACC, the precursory substance of ethylene, reducing the ethylene synthesis which is responsible for inhibiting root growth [59, 91]. The observed plant response to auxins is cell growth, structure of root and stem, vascular growth and development in tissue culture, increased protein, and synthesis and polymerase activity of RNA [10, 90–93]. Auxins are critical to plants, and regulate and manage many developmental processes from embryogenesis to senescence. Of the various plant hormones, auxins acting as the master control mechanism can be considered directly and indirectly responsible for most of the plant development patterns as the most effective regulator of plant processes [94, 95]. Previous studies demonstrated that exogenous IAA influence root architecture, elongation and root surface area, play important roles on the regulation of C–N metabolism, and enhance the conversion of inorganic N to amino acids [96].

Effect of External IAA Applications on Medicinal and Aromatic Plants

Plant growth regulators can affect the biochemical pathways and physiological processes, and can also change the plant metabolism as well as essential oils biosynthesis. It affects the amount and the components of essential oil when applied externally. The effects of growth regulators on plant are likely to change the path of terpenoid biosynthesis and create a stress factor that stimulates defense responses. Auxins regulate most of the physiological activities and growth in plants [77]. On the other hand, IAA can also protect bacteria against environmental stresses [16]. It has been determined that IAA application increased nerol and geraniol in *Melissa officinalis* [97], aromadendrene, β-selinene, and α-humulene in *Sambucus ebulus* [98], the content of α-bisabolol oxide in *Chamomile recutita* [99], the content of linalool in *Ocimum basilicum* [100], the carvacrol and thymol content *Lippia origanoides* [101], and the yield of essential oil in *Ocimum gratissimum* [102]. It has been determined in some previous studies that plant growth regulators increased the herb yield of basil, fenugreek, and coriander plants [103, 104];

affected monoterpenes in *Ocimum basilicum* and *Lavendula dentata* plants [102, 105]. It has been reported that auxin and cytokinins increased certain components in *Melissa* oil [97], similarly, the application of NAA and IAA increased the essential oil in *Mentha piperita* [106]. In addition, it has been shown that cytokinins stimulated the metabolism and accumulation of essential oil, especially monoterpenes in *Mentha piperita* L. and *Salvia officinalis* L. plants [107]. Studies on the effect of plant tissue culture and plant growth regulators on the effect of essential oil profile, composition, and yield have been shown to affect the secondary metabolites [97, 108, 109]. In some other studies, it has been seen that the applications of external hormone affected the main components of essential oil [110, 111]. Roots of medicinal *E. maritimum* growing in auxin-supplemented media regulate in vitro morphogenesis and increase phenolic acid and triterpenoid saponin accumulation [112]. The applications of IAA increased the thymol content in *Thymus vulgaris* oil [110]; content of β–pinene, camphene, and caryophyllene in *Alpinia zerumbet* [111]; rooting, root length and soil surface overgrowth in *Melaleuca alternifolia* plant [113]; yield of essential oil in *O. gratissimum* [92] and in the aromatic grasses of *Cymbopogon martinii* and *C. winterianus* [114]; contents of neral and 1,8-cineole in *Lippia citriodora* [104], and number and weight of root in *Salvia fruticosa* plant have also been determined [115].

Effect of IAA-Producing Bacteria on Medicinal and Aromatic Herbs, Spices, and Seed Crops

Agricultural applications may change the amount of active substance and chemical composition in medicinal and aromatic plants. The plant growth-promoting bacteria were found to have a great potential for use as bio-inoculants to increase production in medicinal and aromatic plants. The production of plant growth hormones has been suggested as one of the mechanisms by which PGPB stimulate plant growth [23, 67]. The PGPB strains may increase the level of root hormone by exogenous production of IAA, cytokinin, and/or other plant hormones in the rhizosphere, which are then absorbed by the root. It is possible that PGPB strains affect root hormone levels by producing IAA and/or other plant hormones in the rhizosphere, which are then absorbed by the root [27]. The preincubation of the *Pseudomonas* sp. and *Azotobacter* sp. lead to the synthesis and release of IAA into the culture medium that could be readily assimilated by the plant. Indeed, when these are co-cultured with shoot cultures of medicinal herb *Swertia chirayita* under in vitro conditions have been reported to increase the number, length, vigor of shoots and roots, and then reduce the use of synthetic plant growth hormones [116]. On the other

hand, the production of IAA by *Azospirillum* sp. has been accepted as the basic factor in stimulating the plant growth [117]. Plant growth-promoting effect of bacterial applications appeared to be related to phytohormone production and a positive relationship between the amount of IAA secreted and plant yield values was also observed for some of the other PGPB [24].

Martinez-Morales et al. [118] reported that *Azospirillum brasilense* strain produces IBA, a substance associated with auxin activity that regulates plant growth. It has been observed that the inoculation of *A. brasilense* stimulates the formation of lateral and adventitious roots, which stimulate the root system through the stimulation of capillary rooting. Bacterial-based microbial auxin production has been shown to play the most effective role on plant growth and development among PGPB action mechanisms. IAA is a secondary metabolite produced by bacteria and mostly affects the root system, and increases the number and size of adventitious roots [119]. It has been stated that IAA-producing bacteria are a very important tool in plant development [120], moreover, stimulate the lateral roots and root hairs, and increase the germination rate and the development of root and shoot [121–123].

In the studies conducted with microorganisms, inoculations of *Glomus fasciculatum*, *Azotobacter chroococcum*, and *A. awamori* have increased the essential oil content, weight of root and stem, and total biomass in *Ocimum* spp. [124], increased the growth of *Ocimum basilicum* with the inoculations of *G. fasciculatum*, *P. fluorescens*, and *B. megaterium* [125], increased the dry weight of root and stem, N, P, K, and essential oil content in *Ocimum basilicum* with the inoculations of *P. putida* and *A. chroococcum* similarly [126]. Similarly, in combination with single and combined PGPB applications or with mycorrhiza inoculations, synergistic effects have been observed in combination with the increase in growth and yield in *Mentha piperita* [127], *Mentha arvensis* [128], *Salvia officinalis* [129], *Silybum marianum* [130], *Foeniculum vulgare* [131], *Ocimum basilicum* [132], *Withania somnifera* [133], *Catharanthus roseus* [134, 135], *Chrysanthemum cinerariifolium* [136], *Calendula officinalis* [137], *Hibiscus sabdariffa* [138], *Origanum majorana* [139], and *Phyllanthus amarus* [140] medicinal and aromatic plants. In previous research carried out in tea plant (*Camellia sinensis*) with PGPB inoculations could be stimulated overall plant growth, including shoot development, plant height, trunk diameter, leaf yield, nutrient uptake, chlorophyll and anthocyanin content, leaf area, and activities of oxidative, catalytic, hydrolytic, and antioxidative enzymes [64, 141–145]. IAA-producing bacteria had significant effects on plant development and corm of *Crocus sativus* [146].

In previous studies, the inoculations of PGPB, also had a positive effect on the essential oil yield in *Ocimum basilicum*

[147], *Mentha piperita* [148, 149], *Anethum graveolens* [150], *Calendula officinalis* [151], *Foeniculum vulgare* [152], *Origanum onites* [153], *Origanum majorana* [139], *Origanum x majoricum* [154], *Pogostemon cablin* [155], *Salvia officinalis* [156], *Satureja hortensis* [157], *Tagetes minuta* [158], and *Pelargonium graveolens* [159]. In addition, certain research findings showed that the applications of IAA could increase plant oil yield [102]. Development and yield of seed and essential oil could be increased with PGPB inoculations in medicinal and aromatic plants such as *Pimpinella anisum* [160, 161], *Coriandrum sativum* [162], *Cymbopogon martini* [163], *Anethum graveolens* [164], *Borago officinalis* and *Nigella sativa* [165, 166], *Foeniculum vulgare* [167–169], *Ocimum basilicum* [170], *Ocimum sanctum* [171], and *Cuminum cyminum* [172]. It has been reported that the IAA production from *Bacillus subtilis* and *Serratia plymuthica* produced the highest indole-3-acetic acid and increase for both the blossoms and the essential oil in chamomile [173].

In many studies conducted on different aromatic plant species, the use of PGPB has been found to have a strategy importance to increase yield and monoterpene production [122, 148, 149, 154, 158]. In addition, increase in the content of several alkaloid and terpenoid compounds of pharmaceutical relevance was demonstrated in medicinal plants following PGPB inoculation [51, 134, 174]. The strong positive relationship between the menthol content and the IAA-producing bacteria showed that auxin production increased the monoterpene accumulation to the mint with high commercial importance [149]. The use of PGPB increases the yield, essential oil components, monoterpene production and accumulation [104, 120, 122, 139, 150, 154, 167, 175], and it affects the biosynthesis of secondary metabolite such as phenolic and flavonoid, and increases the main components of essential oil [156].

It has been determined that the inoculation of plant growth stimulator namely, *P. fluorescence* increased alkaloid content and biomass yield in *Catharanthus roseus* [134]; phosphate solubilizing bacteria increased the grain yield in the medicinal species of *Phyllanthus amarus* [176]; *Azotobacter* and *Azospirillum* bacteria increased plant height, fresh, and dry weight of root in *Salvia officinalis* [177]; *Azotobacter* inoculation increased essential oil ratio in *Rosmarinus officinalis* [178], and herbage and oil yield in *Mentha piperita* [179]; single and combination of *Pseudomonas pseudoalcaligenes* and *Bacillus pumilus* enhanced photosynthetic leaf area, chlorophyll and carotenoid content, leaf-stem ratio and oil yield, menthol, and the total phenolic content under normal condition in *Hyptis suaveolens* [180]; the combined inoculation of mycorrhizal *Azotobacter* fungi with *Azospirillum* and *Bacillus* bacteria increased the total biomass production in *Cymbopogon martinii* species [163]; inoculation with *Serratia liquefaciens* enhanced carvacrol

in *Origanum syriacum* subsp. *sinaicum* [181]; rhizobacteria interactions may alter the alkaloid composition in *Datura stramonium* shoot [182] and total ginsenoside content in *Panax ginseng* [183] and biological fertilizer applications significantly increased the development of *Thymus vulgaris* species [184]. PGPR inoculation has been reported to have a positive effect on essential oil yield and phellandrene main compounds of essential oils in *Rosmarinus officinalis* under normal and salinity conditions [185].

Inoculation with *P. fluorescens* increased the main components in *M. piperita* oil such as the amount of pulegone, menton, menthol, and menthofuran [148]. The full interaction of bacteria with plants stimulates the secondary metabolite response [139, 154]. Inoculation of the *Origanum majorana* plant with *P. fluorescens* could increase the yield of essential oil. Bacteria are encouraged to stimulate the plant growth hormones, produce essential organic compounds, dissolve phosphate, oxidize the sulfur, increase nitrate intake and root permeability, and also combine plant growth with bacterial volatiles [148].

In the studies conducted on *Ocimum basilicum*, it has been shown that the efficiency of the glandular hair and essential oil yield can be increased by PGPB applications [147], and the content of α-terpineol and eugenol can also be increased from the oil components along with the yield of essential oil [122]. It has been noted that the biological fertilizer caused an increase in components of α-pinene, β-pinene, limonene, 1,8-cineole, linalool, camphor, β-terpineol, borneol, terpinene-4-ol, carvone, thymol, carvacrol, linalyl acetate, geranyl acetate, β-caryophyllene, and caryophyllene oxide in *Rosmarinus officinalis* plant [178]. The inoculations of *Origanum x majoricum* with *P. fluorescens*, *B. subtilis* and *A. brasilense* have been found to increase the yield of essential oil and the biosynthesis of the components of essential oil such as cis- and trans-sabinene hydrate, γ-terpinen, carvacrol, and thymol [154]. Essential oil, dry herbage and leaf yield, chlorophyll content, and biosynthesis of major essential oil components such as carvacrol, thymol, linalool, and borneol of *Origanum onites* were significantly affected by inoculation with effective IAA-producing, N_2-fixing, and P solubilizing PGPR species such as *P. fluorescens*, *P. putida*, *B. subtilis*, and *P. polymyxa* [153]. It has been determined that the biological fertilization increases the quality as well as the yield in *Anethum graveolens* [150] and in *Chrysanthemum cinerariifolium* [136].

Santoro et al. [148] reported that the plant hormone-producing bacterial inoculations (*P. fluorescens*, *B. subtilis*, *A. brasilense*) stimulate the biosynthesis of secondary metabolites as well as influencing the flow and specific stages of the path of monoterpene metabolism in *Mentha piperita* plant. In *Coriandrum sativum*, PGPB inoculations were determined to increase geranyl acetate, limonene, and beta pinene content in essential oil [186]; and bacterial biological fertilizers were determined to increase the leaf area index, total chlorophyll content, and the weight of fresh stem of *Sideritis montana* [187]. In *Tagetes minuta* aromatic plant, the inoculations of *P. fluorescens* and *A. brasilense* were found to increase essential oil yield and total phenolic content, and also were important in the accumulation of secondary metabolites [158] and *P. monteilii* PsF84 and *P. plecoglossicida* PsF610 increased the dry biomass of stem, dry root weight, yield of essential oil and chlorophyll content; changed oil composition; and increased the content of citronellol and geraniol of *Pelargonium graveolens* cv. Bourbon [159].

The applications of bacteria were significantly affected the plant growth, oil content and yield in *Calendula officinalis* [151]; in *Mentha piperita*, the root and stem biomasses, leaf area, number of nodes, and densities of hair were increased, and significant quantitative and qualitative changes have been shown in monoterpenes, and the components (pulegone, menton, menthol, 1,8-cineole, and linaol) of essential oil [175]. The increased monoterpene content observed in inoculated plants in these studies may result from growth-promoting substances secreted by PGPB that affect plant metabolic processes. The fresh stem weight, number of glandular hair, dry weight, yield of essential oil, and the biosynthesis of main components in *Mentha piperita* were increased with PGPB inoculations, a positive correlation has been seen between bacterial IAA production and menthol content [149] and root and stem biomass, P content of leaf, yield of essential oil, total phenolic and flavonoid content; and cis-thujene, camphor, and 1,8-cineole from the main components of essential oil have been increased in *Salvia officinalis* [156]. It has been found that the density of glandular trichomes in peppermint inoculated with IAA-producing bacteria is higher and that volatile oils of aromatic plants are generally associated with the total number and distribution of glandular trichomes where the oil components are synthesized and stored [149, 188]. On the other hand, the number and diameter of glandular varices have been reported to affect the oil yield of *Mentha piperita* [179]. PGPB-hosting plants are correlated with nutritional status, and factors that increase dry matter production, affect the interrelationship between primary and secondary metabolism, and leading to increased biosynthesis of secondary products. In addition, increased secondary metabolite production may be directly related to improved nutritional status and primary metabolism of plants after PGPR inoculation.

Effect of IAA-Producing Bacteria on Medicinal Roots, Tubers, Bulbs, and Rhizomes

Bacterial IAA plays a major role in the development of the host plant root system. Auxins have an effect on the whole plant; in particular, IAA is synthesized by microbe mostly

affects the root system, increases the size and number of adventurous roots, and leads to a significant increase in the number of branches and hence the surface area in soil contact [119, 189]. Inoculations with the phytohormone-producing bacteria produced the highest root weights and total root numbers and encouraged adventitious root formation. Root growth is a key auxin-regulated process for plant development. Patten and Glick [61] reported that the IAA, produced from *Pseudomonas putida* by indole pyruvic acid pathway, had a direct positive effect on the root development. Bacterial IAA can attract more rhizosphere bacteria by increasing more amount of root exudation, stimulates the development of the host plant root system, modify the architecture of the root system, and plays a very important role in bacteria-plant interactions.

Bacterial phytohormone production, especially IAA production, is widely distributed among plant-associated bacteria and is still considered the primary mechanism that enhances the growth and yield of plants [190]. Therefore, a number of IAA-producing microorganisms such as *Bacillus*, *Paenibacillus, Lysinibacillus*, *Burkholderia*, *Acetobacter*, *Acinetobacter*, *Aeromonas*, *Azotobacter*, *Agrobacterium*, *Alcaligenes*, *Chryseobacterium*, *Herbaspirillu*m, *Micrococcus*, *Microbacterium*, *Klebsiella*, *Lactobacillus*, *Enterobacter*, *Flavobacterium, Pantoea*, *Rhizobium*, *Rhodobacter*, *Serratia*, *Stenotrophomonas*, and *Pseudomonas* have been isolated from the various medicinal roots, tubers, and rhizomes plants including turmeric, ginger, shallots, ashwagandha, picrorhiza, Jerusalem artichoke, ginseng, and valerian [34, 75, 76, 190–200].

IAA production from *Pseudomonas* has been reported to significantly increase the amount of valerenic acid in the root extract of *Valeriana officinalis* [201]. Endophytic IAA-producing bacterial strain *Pseudomonas* sp. enhanced the nutrient level in soil and growth of medicinal *Withania somnifera* [195]. On the other hand, the co-inoculation of salt-tolerant *Mesorhizobium* sp. with the IAA-producing *Pseudomonas extremorientalis* TSAU20 strains have been reported to alleviate the salt stress of Chinese liquorice (*Glycyrrhiza uralensis*), and increase plant growth, shoot and root weights [202]. It has been reported that the best IAA-producing *Enterobacter* sp. N10 performed best in both root and shoot dry mass growth in Jerusalem artichoke [203]**.** Auxin production of bacterial isolate is also potential to promote shallot (*Allium ascalonicum*) growth, bulb dry weight and bulb dry biomass weight, leaf number, and the number of bulbs tillers [204]. IAA-producing *Pseudomonas poae* inoculation enhanced *Astragalus mongholicus* seedling root biomass and root shoot ratio, and accumulations of calycosin-7-O-glucoside and ononin in the medicinal part root under drought stress conditions [205].

Inoculation of *Curcuma longa* with IAA-producing *Bacillus* spp.[196, 206], and with *P. fluorescens* [194] increased plant growth, the fresh rhizome biomass, morphological yield, turmeric production, and its major bioactive component, curcumin. Combined inoculation of *Azospirillum*, *Azotobacter*, *Pseudomonas,* and *Bacillus* increased plant height, root length, and alkaloid content in *Withania somnifera* [133]. Similarly, inoculation with PGPR showed significantly improved growth and yield in *Withania somnifera* [207]; and increased not only plant height, root length and weight, but also root activity and the content of total ginsenoside a standard on ginseng quality in *Panax ginseng* [183]. Due to the close relationship of root-associated bacteria with root cells, it has the potential to contribute directly to the composition and quality of vetiver (*Chrysopogon zizanioides*) oil, which is the ability to produce essential oil in its roots [208]. Furthermore, Vollú et al. [209] demonstrated that PGPR might contribute to plant growth promotion and improvement of the production of essential oil in vetiver. Inoculation with IAA-producing bacteria increased the shoot and root dry weight [198], tuber numbers and weight, and inulin content in tuber in *Helianthus tuberosus* [210], and could promote the growth in ginger plant [190].

Conclusion

In recent years, the importance of secondary metabolites has become an important area of interest, especially in the production of bioactive and commercially valuable plant metabolites used in particularly, medicinal compounds, agrochemical, pharmaceutical, flavor and fragrances, dye and pigments, and food additives. Although, such studies are still in their initial stage, inoculation with PGPB produced a certain increase in stomatal density and also in the levels of secondary metabolites in several aromatic plant species. Biological nitrogen fixation and microbial production of phytohormones were observed to be the major factors responsible for plant growth improvement by PGPB, which help in the development of efficient root system for enhancing soil nutrients and water uptake. Inoculating medicinal and aromatic plants with root-associated bacteria enhances plant growth, development, and secondary metabolite production through increased nutrient and moisture availability. One of the most prominent features of plants inoculated with auxin-producing PGPBs is the modification in the root morphology and development. Bacterial IAA play central regulatory role in cell elongation, stimulate rooting and root formations, increasing the number of roots and root hairs, also number and development distribution patterns of glandular trichomes, part of the biosynthetic machinery that rapidly and efficiently converts imported carbohydrates into essential oils. Thus, plant growth-promoting bacteria promote root growth by increasing root surface area, which

in turn promotes nutrient uptake thereby indirectly stimulating plant growth positively.

Inoculation of IAA-producing PGPB increased growth, biomass, photosynthesis and their pigments, nutrients, root branching and length, and also the total amount of essential oil and its yield, the production monoterpenes and biosynthesis of major essential oil components, and production of volatile secondary metabolites such as thymol, geraniol, α-terpineol, caryophyllene, phenols, ortho-dihydroxy phenols, tannins, flavonoids, and alkaloids; induce secondary metabolites responses, influence pathway flux of specific steps of monoterpene metabolism and phenolic compound pathways. The use of growth-promoting bacteria reduces the need for chemical fertilizers and pesticides applied to cultivated medicinal and aromatic plant species. Only a limited number of commercial rhizospheric microorganisms are currently marked for medicinal and aromatic plants. Bacterial inoculants are an efficient biotechnological tool for stimulating plant growth parameters and secondary metabolism in aromatic plants and future studies of their activities will increase our understanding of certain adaptive processes that are poorly understood at present era.

The action of IAA- producing PGPR on the growth and essential oil and their components in medicinal aromatic plants remain a focus area for future research. Although there is increasing interest in IAA-producing PGPB inoculations due to some exciting new findings, much less is known about the potential to associate PGPB with other economically important medicinal and aromatic plants, and only a few studies are found in literatures. Bacterial inoculants are an effective biotechnological tool for stimulating secondary metabolism in plants, but much less is known about the biosynthesis, regulation, and localization of terpenes synthesized in roots and whole plant. Microbial strategy is an attractive way for medicinal herbs and roots crops, but little is known about the potential and capabilities of PGPR to produce and increase plant secondary metabolites, and processes affecting the accumulation of monoterpenes and phenolic compounds.

In several medicinal and aromatic plant species consumed without further processing, the absence of any synthetic compounds in the harvested product and the use of chemical inputs in the production are of great importance in the food and pharmaceutical industries, so developing growth-promoting strategies involving PGPR and bio-fertilizers is the most ideal strategy. Further studies are needed to investigate possible mechanisms, by which bacteria increase phytochemical components in medicinal plants at the tissue, cell or molecular level, and to determine and regulate the main molecular mechanisms that drive the increase in essential oil after PGPB inoculation. In research, it may be desirable to isolate and screen new, valuable, environmentally adapted and natural strains to

understand the mechanisms of various plant–microbe interactions that are able to trigger the biosynthetic pathways of bioactive compounds to enhance plant growth and secondary metabolite. Additionally, the modification, proliferation, and extraction of the production of medicinally important volatile constituents and secondary metabolites in medicinal and aromatic plants through plant cell and tissue culture technology can be used as an alternative and useful production system in the future. Further research is needed to clarify the role of other ecological factors, such as competition between root colonization sites and competition between PGPB strains and indigenous soil microflora, and characterize the mode of actions of these bacterial isolates in the metabolic pathway of essential oil production, and evaluate their field scale.

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