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REVIEW ARTICLE

The potential of bacterial endophytes on orchids

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Abstract

Orchids are one of the most exquisite and diverse plant species in nature. The seeds of orchids are non-endospermic and, therefore, dependent on endophytes for germination, growth and adaptability. Orchids are prized for their beauty and therapeutic and culinary qualities by naturalists and the general public. Many orchid species are now endangered or vulnerable due to collectors' eagerness to take them. Current studies on orchids have concentrated on isolating and identifying the mycorrhizal and non- mycorrhizal endophytes that either directly or indirectly help orchids to grow, develop and produce beneficial secondary metabolites. In orchids, bacterial endophytes play an essential role in the formation of mycorrhizae and the stability of relationships between plants and fungi. Endophytic bacteria can grow in orchids by producing phytohormones, doing photosynthesis, fixing nitrogen, promoting the mineral nutrition cycle, forming siderophores and producing diverse beneficial metabolites to improve biomass production, stress tolerance and biocontrol of potential phytopathogenic fungal species. This article examines how endophytic bacteria are associated with orchids and their potential growth-promoting abilities.

Keywords: bacterial endophytes; orchids; orchid endophytes; PGPR

Introduction

The orchid family represents the second largest angiosperm family, with over 900 genera and 27000 species worldwide (1). They have evolved in various captivating ways to survive extreme weather conditions, acquire nutrients and attract pollinators (2). Due to their decorative, culinary and therapeutic uses, orchids are widely grown in domestic and foreign cities. In particular, the orchid plant's roots, foliage and pseudo-bulbs can treat conditions including rheumatism, respiratory illnesses, nausea, piles, inflammation, viral infections and even cancer (3).

Orchids produce many highly reduced, microscopic seeds per capsule, but only 0.2 – 0.3 % germinate in nature, while thousands die (4). A symbiotic relationship between orchid seeds and mycorrhizae is required for orchid propagation (5). As mycorrhizae provide most minerals, nutrients, vitamins and water for orchid germination and seedling development, they differ in how they relate to their orchid hosts (6). *In vitro*, symbiotic germination has been used for orchid propagation. Sustainability is crucial in preventing declines in orchid biodiversity, scenic attractiveness and therapeutic benefits. In orchids, microbial communities provide nutrients and enhance immunity through symbiotic relationships. In nature, most plants work in symbiotic harmony with other species; some depend on bacterial or fungal interactions for survival. Still, successful propagation requires extensive knowledge of orchid-mycorrhizal interaction and the ability to isolate and grow the fungus, which can be time-consuming (7-9).

Orchids have not been extensively explored for their endophytic bacteria, even though some commercially valuable epiphytic orchids, such as *Vanilla* spp. (10), *Dendrobium* spp. (11) and *Cymbidium* spp. (12), contain endophytes. These microorganisms can promote plant growth, particularly in acclimating micro-propagated seedlings (13). Endophytic bacteria may promote plant growth by producing indole acetic acid (14) and solubilizing inorganic phosphate (15).

This review explores the potentiality of bacterial endophytes on orchids and their importance, roles and implications in orchid ecology, growth and conservation. It also discusses the limited research in the field of orchid-associated bacterial endophytes and points out the need for further investigations in this area. The review also explores the potential of bacterial endophytes to benefit orchids in various ways, such as promoting plant growth, enhancing stress tolerance and possibly contributing to the discovery of bioactive compounds with pharmaceutical applications.

Orchid endophytes

Endophytic bacteria have been discovered in various environments, including tropical, temperate, aquatic, xerophytic, deserts, Antarctica, geothermal soils, rainforests, mangrove swamps and coastal forests (16, 17). Microbial endophytes have also been extensively examined in orchids (10-12). Orchids and mycorrhizal fungi interact much and the distribution of these fungi and orchids is interrelated (18). Mycorrhizal associations are essential for orchid survival. Most microbiological studies have focused on them while disregarding the possible contributions of other microbial partners

(19,20). There are also endophytic bacteria that can form symbiotic relationships (21). Some bacteria that inhabit orchids include *Streptomyces* spp. (22), *Bacillus* spp. (23), *Erwinia* spp., *Pseudomonas* spp. (24), *Flavobacterium* spp. (25), *Sphingomonas paucimobilis* ZJSH1 and *Streptosporangium oxazolinicum* (24). Only a few studies on the interactions between bacteria and orchids have shown the potential of bacteria as a biological tool for conserving orchids and generating bioactive compounds (24, 26). However, some bacterial and fungal species were thought to be the best sources for researching the interactions between orchids and microorganisms and how they affect the evolution of orchid species (27).

Bacterial endophytes

Few studies focus on orchid bacterial endophytes. In orchid roots and leaves, bacterial endophytes have been isolated aher surface sterilization; some isolated bacteria increased seed germination (28, 29). Root associated bacteria (RAB) interact with plants, colonize root compartments and control plant host function (30). These are recruited based on host genotype, metabolic profiles, root exudates and soil physicochemical properties (30). They facilitate plant growth by acquiring nutrients, supplying hormones, protecting against infections and reducing abiotic stressors (Fig. 1) (31). Duponnois and Garbaye published insight into mycorrhizal and bacterial associations in orchid root tissues (32). They demonstrated that *Pseudomonas fluorescens* BBC6 aids in the formation of mycorrhizae and gave the name "mycorrhiza helper bacteria" (MHB). MHB releases active substances or biomolecules in stress response, which promotes mycelia development, root colonization and root growth (33). Endophytic rhizobacteria, including *Paenibacillus lentimorbus* and *P. macerans,* were isolated from the meristems of *Cymbidium eburneum* (26). Strains of *Sphingomonas* sp., *Agrococcus* sp. and *Mycobacterium* sp. promoted orchid germination and were isolated from *Dendrobium moschatum* (24). The study by Yu *et al.* amplified endophytic bacteria from the roots of *D. officinale* belonging to the genera *Burkholderia, Rhodanobacter, Pseudomonas* and *Sphingomonas* (34). The major endophytic bacteria of *Cymbidium* orchid are *Bacillus thuringiensis*, *Burkholderia cepacia, B. gladioli, Herbaspirillum frisingense, Pseudomonas stutzeri, Rhizobium cellulosilyticum, R. radiobacter* and *Stenotrophomonas maltophilia* (12). Endophytic bacteria from *Spiranthes spiralis*, *Serapias vomeracea* and *Neottia ovata* were identified using the 16S rRNA gene. These include *Pseudomonas, Pantoea, Rahnella, Staphylococcus, Sphingomonas, Microbacterium, Streptomyces, Fictibacillus* and *Bacillus* (35). The endophytes like *Paenibacillus taichungensis, P. pabuli, Enterobacter* sp., *Rhizobium* sp. and *Pseudomonas* sp. were isolated from *Cattleya walkeriana* (37).

Importance of endophytic bacteria

In orchids, endophytic bacteria can colonize symbiotically without harming their hosts. In addition to exchanging metabolites and sharing physiological processes with the host plant, these microorganisms can reside within plant tissues, including roots and leaves (38). In orchid roots, bacteria interact with fungi and orchid root cells to maintain symbiosis by producing plant growth-promoting metabolites and indirectly by inhibiting fungal growth that could harm the plant (31). There are several plant growth-promoting rhizobacteria (PGPR), such as *Acinetobacter, Arthrobacter, Azospirillium, Azotobacter, Bacillus, Burkholderia, Clostridium, Enterobacter, Erwinia, Flavobacterium, Klebsiella, Pseudomonas, Serratia* and *Rhizobium* (38). These bacteria may be able to stimulate plant host growth through the production of phytohormones and

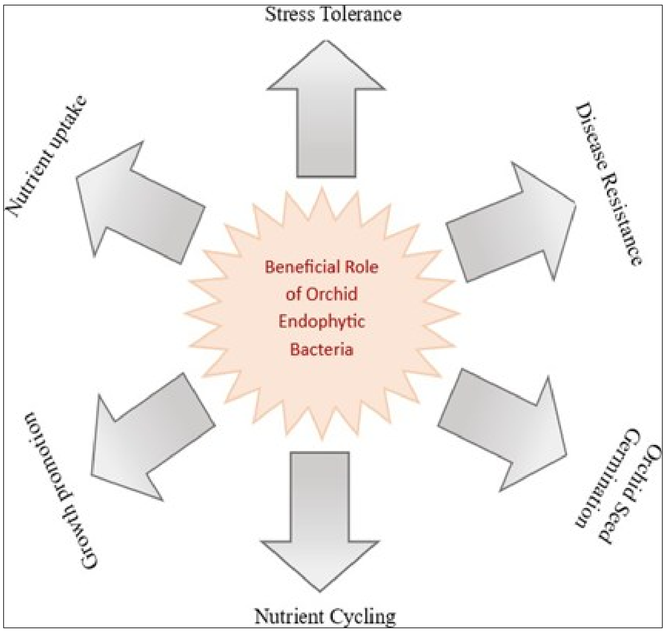

Fig. 1. The beneficial role of bacterial endophytes on orchid.

through the production of ACC deaminase, which effectively lowers plant ethylene concentrations (39) (Fig. 2). By reducing the inhibitory effects of various phytopathogens, PGPR facilitates plant growth and adaptive capacities through nitrogen fixation (40), assistance in acquiring phosphorus (41) and essential minerals (42), improved water uptake, or acting as a biocontrol agent (Fig. 2) (43). Endophytic bacteria are less investigated for their metabolic potential (44, 45) (Table 1). Endophytes synthesize bioactive compounds such as paclitaxel from *Taxomyces andreanae,* endophytic fungi isolated from pacific yew (*Taxus brevifolia*) (46) help the host plant to develop resistance against pathogens that are used in pharmaceutical industries as antibiotics (47) and anticancer agents (48), anti-virals (48), diabetes medications (48). Endophytic bacteria isolated from *Vanda cristata* contain bioactive metabolite ethyl iso-allocholate with antimicrobial properties that contribute to plant fitness by overcoming biotic stress (23).

Conservation implications of orchid by orchid-associated bacteria

It is challenging to conserve orchids due to their strong biotic relationships and tiny seeds that require mycorrhiza to germinate. Arbuscular mycorrhizal fungi (AMF), one of these advantageous microbes, have symbiotic relationships with over 80 % of the species of vascular plants (42) and are regarded as an essential class of soil microorganisms that enhance plants' uptake of phosphorous (49). AMF may also increase a plant's resistance to abiotic stressors (50) and its ability to defend itself against infections. Mycorrhiza helper bacteria (MHB) facilitate the establishment and the functioning of the symbiotic association of AMF by stimulating spore germination (51), mycelial growth (52), root colonization (53), sporulation and by reducing stresses that could impact AMF symbiosis. Also, they can stimulate root exudates, activating AM hyphae and, therefore, a higher rate of mycorrhizal root colonization (54).

Orchid plant growth promoting rhizobacteria

Plant growth - promoting rhizobacteria (PGPR) has been continuously reported as a plant root colonizing endophytic bacterium that helps plants absorb nutrients and minerals from the soil and plays a vital role in mineralizing organic phosphorus (55) and iron, fixing di-nitrogen (56) and producing phytohormones and bio regulators (57). An endophytic bacteria isolated from *Cymbidium*

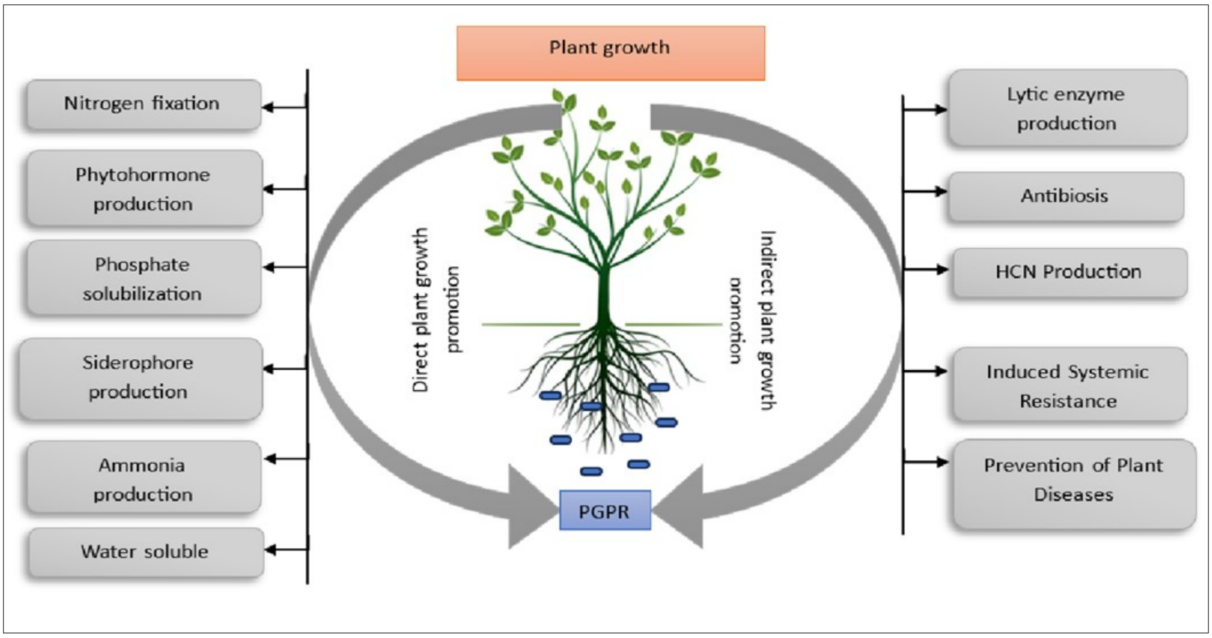

Fig. 2. Schematic diagram about the mode of action of PGPR in promoting plant growth.

Table 1. Bioactive metabolites from endophytic bacterial source

Sl.No.	Name of the endophytic bacteria	Name of the metabolites produced	Name of the host plant	References
1	*Streptomyces* sp.	Eicosanoic acid	*Vanda corulea*	22
2	*Streptomyces* sp.	Pyrazole-5-carboxylic acid	*V. corulea*	22
3	*Streptomyces* sp.	phenol,2,4-bis-(1,1-dimethyl ethyl)	*V. corulea*	22
4	*Streptomyces* sp.	Cyclononasiloxane	*V. corulea*	22
5	*Streptomyces* sp.	1-Deoxy-d-mannitol	*Renanthera imschootiana*	22
6	*Streptomyces* sp.	phenol,2,4-bis-(1,1-dimethyl ethyl)	*R. imschootiana*	22
7	*Streptomyces* sp.	Benzoic acid, 3-(2-methoxyethyl) heptyl ester	*R. imschootiana*	22
8	*Streptomyces* sp.	1-Nonadecene.	*R. imschootiana*	22
9	*Streptomyces* sp.	1,2-Benzenedicarboxylic acid, bis (2-methyl propyl) ester	*R. imschootiana*	22
10	*Bacillus* sp.	6-acetyl-beta-d-mannose	*V. cristata*	23
11	*Bacillus* sp.	ethyl iso-allocholate	*V. cristata*	23

orchid contributes to plant growth and biomass production (12). A study by Alibrandi *et al.* analyzed the diversity of endophytic bacteria associated with *Neottia ovata, Serapias vomeracea* and *Spiranthes spiralis* and determined the importance of these bacteria for orchid development (35). In cultivated tropical orchids genera of *Calanthe, Acampe* and *Dendrobium*, heterotrophic and phototrophic bacteria were abundant. The isolated strains were shown to fix nitrogen from the orchid's surrounding cyanobacterial community and to produce Indole acetic acid (IAA) from heterotrophic bacteria (58). It was also found that some strains of orchid- associated bacteria could promote symbiotic germination of *Cymbidium goeringii* (59). Plants obtain iron via root- mediated degradation by producing siderophores and chelating agents (60). In addition, some beneficial RABs, *Bacillus*, *Rhizoctonia*, etc., make phosphorus more available by acidifying (61), chelating, or releasing phosphatases (62). Nitrogen is fixed by nitrogenase activity, which makes it easier for plants to use (63) (Table 2).

Several strains of *Sphingomonas, Agrococcus, Mycobacterium* and *Bacillus* produce IAA, which facilitates the germination of host orchids (31). *Sphingomonas paucimobilis*, an endophytic bacterium from *Dendrobium officinale* roots, fixes atmospheric nitrogen and increases seedling growth. Seedlings inoculated with *S. paucimobilis* contain high amounts of salicylic acid, IAA and abscisic acid, which may promote growth or provide systemic resistance to biotic stresses (64).

Conclusion

The article focuses on the importance of endophytic bacteria in orchid ecology, particularly their symbiotic relationships and potential contributions to orchid growth, development and conservation. Orchids are fascinating plants with remarkable adaptations to survive in various environments and their interactions with mycorrhizal fungi have been extensively studied. However, the role of bacterial endophytes has been relatively understudied, despite some notable research highlighting their significance, the diversity of endophytic bacteria found in various orchid species, including important genera like *Bacillus*, *Streptomyces*, *Pseudomonas* and *Sphingomonas*. These endophytic bacteria have been shown to facilitate plant growth by providing nutrients, promoting hormonal balance and enhancing the resistance to biotic and abiotic stresses

Moreover, some endophytic bacteria have been found to produce bioactive metabolites with potential pharmaceutical applications, including antibiotics, anti- cancer compounds, anti-virals and diabetes medications. These findings indicate that orchid-associated bacteria play essential roles in plant health and hold promise for future drug discovery and biotechnological applications. Conservation implications are also discussed, as orchids face challenges in their conservation due to their complex relationships with mycorrhizal fungi and the low germination rates of their tiny

Table 2. Role of endophytic bacteria in orchids.

Sl.No	Orchid species	Endophytic bacteria	Role in plant growth and development	References
1	*Paphiopedilum appletonianum*	*Streptomyces* *Bacillus* *Pseudomonas* *Burkholderia* *Erwinia* *Nocardia*	IAA production ●The biological action of microbial IAA was demonstrated by treating kidney bean cuttings with bacterial supernatants, significantly stimulating root development and growth.	7
2	*Pholidota articulata*	*Pseudomonas* *Flavobacterium* *Stenotrophomonas* *Pantoea* *Chryseobacterium* *Bacillus*	IAA production ●The biological action of microbial IAA was demonstrated by treating kidney bean cuttings with bacterial supernatants, which significantly stimulated root development and growth.	7
3	*Dendrobium moschatum*	*Sphingomonas* *Mycobacterium*	IAA production ●Inoculation of *D. moschatum* seeds with *Sphingomonas* sp. and *Mycobacterium* sp. significantly improved orchid seed germination even in the absence of plant growth stimulators or mycorrhizal fungi	14
4	*Cymbidium eburneum*	*Paenibacillus lemtimorbus* *P. macerans*	Plant growth promoters ●Endophytic *P. lemtimorbus* and *P. macerans* strains significantly increased biomass in *Cattleya* seedling shoots and roots compared to non-inoculated seedlings.	13
5	*Cymbidium* sp.	*Bacillus* *Burkholderia* *Herbaspirillum* *Pseudomonas* *Rhizobium*	Plant growth promoters ●Isolated *Herbaspirillum* and *Stenotrophomonas* increased the dry matter in *Cymbidium* sp. plants by 26% and 29%, respectively, compared to the control.	15
6	*Neottia ovata*	*Cutibacterium* *Rhodanobacter* *Pseudomonas* *Sphingomonas*	Plant growth promoters ●Most bacterial isolates demonstrated some potential Plant Growth Promoting characteristics, such as nutrient solubilization, ACC deaminase activity and IAA production.	16
7	*Serapias vomareceae*	*Cutibacterium* *Pseudomonas* *Leutibacter*	Plant growth promoters ●Most bacterial isolates demonstrated some potential Plant Growth Promoting characteristics, such as nutrient solubilization, ACC deaminase activity and IAA production.	16
8	*Spiranthes spiralis*	*Mycobacterium*	Plant growth promoters ●Most bacterial isolates demonstrated some potential Plant Growth Promoting characteristics, such as nutrient solubilization, ACC deaminase activity and IAA production.	16
9	*Cattleya walkeriana*	*Paenibacillus* *Enterobacter* *Rhizobium* *Pseudomonas*	Plant growth promoters ●These endophytes were inoculated in acclimatizing seedlings of *C. walkeriana* obtained from micropropagation and have a potential role as plant growth promoters, as well as in morphological alterations, nutrient uptake and improved antioxidant enzyme activity.	17
10	*Dendrobium officinale*	*Sphingomonas paucimobilis*	Plant growth promoters ●Nitrogen fixation and the secretion of plant growth regulators such as IAA, Zeatin, Salicylic acid and ABA offer *S. paucimobilis* growth-promoting capabilities that could be used for commercial cultivation of D. officinale.	25
11	*Dendrobium* sp.	*Burkholderia* *Bacillus* *Paraburkholderia* *Kluyvera* *Rouxiella*	Antimicrobial activity ●Antimicrobial activity against *Athelia rolfsii*, *Myrothecium roridum* and *Pectobacterium carotovorum* by the Kirby-Bauer method showed activity against at least one pathogen in this study.	26

12	*Epipactis* sp.	*Bacillus* *Pseudomonas*	Plant growth promoters •Endophytic bacteria, particularly those categorized as prototrophic organisms, can boost the growth and development of Epipactis orchids, particularly those grown in nutrient-poor soils.	27
13	*Epipactis* sp.	*Bacillus* *Clostridium* *Pseudomonas* *Stenotrophomonas*	Plant growth promoters •Endophytic bacteria may stimulate the growth and development of *Epipactis* orchids, especially those that grow in nutrient-poor soil.	28
14	*Dendrobium nobile*	*Pseudomonas fluorescens* *Klebsiella oxytoca*	IAA production •*K. oxytoca* and *P. fluorescens* produced the highest amounts of auxin in nitrogen-limiting and NO3-containing environments. Bacterization of *D. nobile* seeds increased their in vitro germination.	29
15	*Doritaenopsis Jiuhboo*	*Mycobacterium*	IAA production •Mycobacterium can synthesize and secrete the plant growth hormone indole-3-acetic acid (IAA). In *Doritaenopsis*, Mycobacterium inoculation enhanced root number and length, plant height, leaf number and leaf length. It also increases seed germination in Doritaenopsis.	30

seeds. Understanding the role of endophytic bacteria in these interactions may offer new avenues for conserving orchids, enhancing their germination success and improving their adaptability to changing environmental conditions. This article highlights the ohen-overlooked role of endophytic bacteria in orchid biology and ecology. Further research could lead to valuable insights into orchid conservation, sustainable propagation methods and the potential discovery of novel bioactive compounds with critical pharmaceutical applications. Orchids, with their captivating beauty and therapeutic qualities, deserve continued attention and research to ensure their preservation and sustainable use in the future.

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Authors' contributions

This study was conceptualized by SS. The draft of this manuscript was written by AA and PR. Resources for the study were provided by SS. Final draft was reviewed and edited by SS and GA. All authors read and approved the final manuscript before publishing.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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