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Review Article

Plant Growth Promoting Endophytic Microorganisms from Orchids for A Sustainable Agriculture

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ABSTRACT
Conventional agriculture practice has heavily relied on chemical fertilizers to increase crop yield. However, long-term application of chemical fertilizers carries tremendous negative impact on the environment and is unsustainable. Hence, the search for an alternative source of fertilizers is required. Orchids are flowers and can be found in tropical countries. The growth and development of orchids are closely tied to the presence of plant growth promoting endophytic microorganisms (PGPM). PGPM harbours various beneficial traits such as potassium and phosphorus solubilization and indole acetic acid and siderophore production which enhance and support plant growth and development. This review article showed that PGPM isolated from orchids could be utilized in conventional agriculture to reduce dependency on chemical fertilizer.

INTRODUCTION
Orchidaceae, commonly known as the orchid family is one of the most diversified monocotyledonous, flowering plant family with over 20,000 species found around the world and approximately 75% are distributed in the tropical region (Cetzal-Ix et al. 2014) . The orchid species, with its significant ornamental value and a diverse range of vegetative and floral features, has piqued the interest of numerous horticulturists and scientists due to its uniqueness (Cetzal-Ix et al. 2014). One of the numerous reasons for the ecological significance of orchid species is their diverse biodiversity and habitat which spans from tree bark to wet areas such as sand dunes (Ma et al. 2016). Biodiversity is described as the variety of flora and fauna found worldwide or in a specific ecosystem. High levels of biodiversity in a region are considered significant and valuable. The presence of diverse orchid species demonstrates that the specific ecosystem provides optimum environment, resulting in a healthy and functional ecosystem. There are approximately 25,000 orchid species that have evolved to become a prominent feature of the world's vegetation (De & Singh 2015). Over 1350 species were classified into 186 genera accounting for 5.98% of the total orchid flora and 6.8% of flowering plants (De & Singh 2015).

ENDEMIC ORCHID
Overhunting of plant biodiversity and pollution due to human activities

contribute to the endangerment of previously dominant life forms because of deterioration of ecosystem. The increase-land use intensity such as logging resulted in a clear a significant negative impact on fish communities. Logging up to two cycles are sufficient to have negative impact on freshwater ecosystems (Wilkinson et al. 2018). Orchids also faced similar threats from human activities (De & Singh 2015). Overharvesting and rainforest deforestation led to the endemic of several species of orchids (Rubluo et al. 1993). Therefore, orchid conservation measures are necessary across all countries to avoid the extinction of orchid biodiversity in the wild.

The tropical and alpine zones such as woody plants, secondary vegetations, floodplains, bamboo and palm thickets, woodland, grassy slopes, and rugged regions are highly prevalent orchid sites (Chowdhery 2004). Two regions, Sikkim and Arunachal Pradesh Himalayas are examples of other home states harboring distribution endemic orchid species (Nayar 1996). Sabah is the key location for orchid diversity, with around 1300 species representing 250 orchid taxa classified as endemic species (Juiling et al. 2020). An evaluation of the International Union for Conservation of Nature's (IUCN) Red List revealed that 136 endemic orchid species are in the areas near the Kinabalu and Crocker Range parks located in North Borneo, Sabah (Juiling et al. 2020). Maximum entropy (MaxEnt) algorithm generated species distribution models for 47 endemic orchid species and gained insights into their adaptive behavior and development through natural selection (Dewar 2010). The findings suggested that approximately 83% of the researched species were imperiled, and urgent conservation efforts are required in areas with significant species diversity to avert orchid species extinction. In Crocker Range National Park located in Sabah, 100 of the park's 341 orchid species are endemic to Borneo, whilst 53 are indigenous to Sabah (Majit et al. 2014). Bulbophyllum is the most recently found genus, followed by Dendrobium and Dendrochilum. *Bulbophyllum neilgherrense* is an epiphytic orchid that has been actively used by the communities of Karnataka to treat a variety of ailments, such as skin allergies and rheumatism (Nair et al. 2018). A study also reported that *Bulbophyllum neilgherrense* possesses analgesic and anti-inflammatory effects in response to radiant heat-induced pain and carrageenan-induced acute inflammation (Nair et al. 2018).

Phalaenopsis amabilis is commonly called as moth orchid, is amongst the most economically significant orchid species in the Orchidaceae family. It is mostly recognized in international trade and the global ornamental market (Ko 2018). *Phalaenopsis* orchids are notable for their unique biological metabolism as they participate in crassulacean acid metabolism (CAM) photosynthesis. They are also recognized for their large, thick leaves and robust flowers (Košir et al. 2004). *Phalaenopsis* is an Indonesian native orchid, giving it the country's national flower due to its dazzling white colour (Semiarti 2018). Stomatal identification of *Phalaenopsis amabilis* demonstrated that it is a type of monopodial orchid with anomocyctic stomata (Zahara & Win 2019).

ORCHIDACEAE FUNGAL AND BACTERIAL ENDOPHYTES

The terminology "Endophyte" relates to microorganisms that reside either partially or their entire life within the plant cells without inflicting any obvious harm of having a symbiotic relationship (Hardoim et al. 2015; Wilson 1995). Endophytes have been thoroughly researched due to their propensity to create biochemicals and exert beneficial effects towards plant growth and development (Chutulo & Chalannavar 2018). Numerous research have been conducted on the biodiversity of endophytes, notably mycorrhizal and bacterial endophytes in orchids. *Penicillium*, *Fusarium*, and *Daldinia* are examples of endophytic fungi derived from traditional medicines (Kuo et al. 2021). Endophytic bacteria such as *Dyella marensis*, *Collimonas pratensis*, and *Luteibacter rhizovicinus* have been associated with terrestrial orchids (Herrera et al. 2020). The colonization and penetration mechanisms of Orchidaceae fungal endophytes (OFEs) differ compared to other fungal pathogens as the OFEs penetrated through the stomata laterally in the cells of the anticlinal epidermal. In comparison, pathogenic endophytes gain entry directly through the cell wall (Sarsaiya et al. 2019). The localization of OFEs are confined along with the intercellular in the shoots, in contrast to pathogens where they grow extracellularly (Sarsaiya et al. 2019).

Mycorrhizal and non-mycorrhizal endophytic microbes have been isolated and characterized from orchid species in order to determine their direct or indirect impact on orchid growth and secondary metabolite synthesis (Pant et al. 2017). The symbiotic relationship between the seeds in orchids with species-specific Basidiomycetes fungus symbionts were reported where germination initiated once the seed receives nourishment from the colonizing fungal symbiont after penetrating the seed that lacks endosperm (Pant et al. 2017). Orchid plants could influence the extent of fungal interaction to fungus colonization which create a symbiotic relationship (Arditti & Pridgeon 1997). Plant growth-promoting endophytes are bacterial endophytes that enhance plant growth via the synthesis of phytohormones such as Indole-3-Acetic Acid (IAA) primarily using the indole acetamide pathway (Arditti & Pridgeon 1997). IAA is naturally abundant phytohormone in plants; the latest mutagenesis and molecular research discovered that IAA is engaged in mediating plant growth (Teale et al. 2006) DNA barcode pyrosequencing observed that Proteobacteria is the prominent genus of endophytic diazotrophic bacteria capable of producing IAA in *Dendrobium catenatum* (Li et al. 2017).

Nitrogen (N) is a key element of plants, particularly chlorophyll, which enables photosynthesis and ensures the healthy growth of plants (Leghari et al. 2016). Numerous endophytic bacteria are capable of fixing nitrogen which provides plants with crucial nitrogen sources and they offer an alternative solution to chemical fertilizers (Puri et al. 2017). Li et al. (2017) discovered that the orchid-associated cyanobacteria in *Dendrobium catenatum* perform nitrogen fixation, ensuring the host plant's ecological stability.

Relationship between Endophytes with Orchidaceae Plants

Orchidaceae is the finest plant family attributed to their nutrition strategy being associated with endophytes (Sarsaiya et al. 2019). *Streptomyces* sp., *Bacillus* sp., and *Erwinia* sp. are examples of bacteria having a symbiotic relationship with orchid which contributed to their resiliency against external harm (Tsavkelova et al. 2007; Yang et al. 2008). However, majority of evidence on orchid-endophytes interactions has centered on terrestrial and temperate orchid mycorrhizal. This is because the majority of orchid species are epiphytic and tropical, hence increasing their relationship with endophytes, particularly endophytic fungi (Salazar et al. 2020). Despite that, the critical role of bacteria in mycorrhizal development was examining the influence of *Laccaria laccata* mycorrhizas and sporocarps on *Douglas-fir* ectomycorrhizal development (Duponnois & Garbaye 1991). The study reported the term "mycorrhiza helper bacterium" (MHB), which has demonstrated that *Pseudomonas fluorescens* BBC6 aids the formation of ectomycorrhiza. Endophytic bacteria are capable of secreting secondary metabolites in response to environmental stress. An endangered orchid species, *Anoectochilus formosanus* (*A. formosanus*) also known as "Jewel Orchid", is well-known for its therapeutic properties due to secondary metabolites produced via mycorrhizal interaction with endophytes (Zhang et al. 2013). The endophytic fungal growth promotes shoot elevation and leaf density in *A. formosanus* by secreting ginsenosides and flavonoids which carries therapeutic effects (Zhang et al. 2013) . Plants and endophytes have a symbiotic relationship through the exchange of nutrients.

A study has reported that mycorrhizal-associated plants acquire phosphate from fungi in exchange for sugar (Al-Karaki & Al-Raddad 1997). Plant growth-promoting endophytic bacterial have been isolated from the leaf of *Vanda cristata* (Shah et al. 2021). The endophyte is capable of producing phytohormones during root colonization and antimicrobial substances that aid in repairing the orchid plant's immunological capacities.

Gastrodia elata (*G. elata*) is an orchid species that are dependent on mycorrhizal fungi for growth in its lifespan it was reported to transition from Mycena, a single-fungus relationship, to Armillaria, another single-fungus relationship (Chen et al. 2019). This transition of different growth phases of *G. elata* also alters the fungal community (Chen et al. 2019). Epiphytic and terrestrial orchid seeds exhibit distinct responses to fungus isolated from roots (Liu et al. 2010). This suggested that epiphytic orchids have a more extensive mycorrhizal association with fungi during the seed germination stage compared to terrestrial orchid species.

Endophytes from Orchidaceae Shoots

Orchidaceae-fungal endophytes (OFEs) occurring on the shoots of orchids have the potential to significantly advance the symbiotic relationships of diverse fungal endophytes with distinct mycota via horizontal transmission into the Orchidaceae (Sarsaiya et al. 2019). Numerous articles have demonstrated the recovery of OFEs from various Orchidaceae species. A study described the association of a broad base of filamentous fungi, *Fusarium* with orchids, as it can reside as pathogens or non-pathogens which could be isolated from the orchid's shoot segments (Srivastava et al. 2018). The non-pathogenic *Fusarium* sp. may behave as a decomposer or a mutualist in orchid plants, such as stimulating seedling growth (Booth 1971; Vujanovic et al. 2000). Orchid seed germination using *Fusarium* isolates from *Cypripedium reginae* revealed the formation of protocorm and induction of seed germination (Vujanovic et al. 2000). Meanwhile a pathogenic *Fusarium* caused progressive increase in orchid infections, impeding the production of high-quality orchids by causing symptoms such as leaf withering (Wedge & Elmer 2008).

Colletotrichum is a fungal endophyte that was isolated from the shoots of *Dendrobium aqueum*. A study has recovered endophytes which exhibit organ specialization, with a greater ensemble in stem sections and only a single endophyte was found in the leaf segments (Parthibhan et al. 2017). Pathogenic endophytes did not cause any significant negative impact on orchids despite their presence (Parthibhan et al. 2017). *Colletotrichum* species are considered a pathogenic fungus which can be found on a diverse variety of ornamental plants, including orchids (Guarnaccia et al. 2021). To ensure that *Colletotrichum* does cause negative infection in host plants, the plants must first be capable of detecting the presence of potential pathogens and afterwards establish a strong defense against the pathogenic invasion (Scherr et al. 2014). Therefore, plant defense mechanism is important for mediating fungal-host plant interactions.

Orchidaceae Roots Endophytes

Several terrestrial genera have their roots structured in the way of a three-layered epidermis when examining a cross-section of velamentous roots (Einzmann et al. 2019). Despite several studies indicating that the operational impacts of a velamen are not significant in terrestrial plants, one study attempted to prove its role by focusing on the roots of epiphytic orchids (Benzing 1996). Bacteria and fungi have been shown to aid plant growth by solubilizing vital phosphorus, phosphate, and nitrogen, as well as being a significant nutrient supplier for orchid seeds germination rate and during the cotyledonary development (Shakeel et al. 2015; Herrera et al. 2020). S. Chen et al. (2019) investigated the role of root associated bacteria (RAB) in wheat maturation and discovered that various bacterial genera were associated with plant ripening in roots when exposed to nitrogen fertilization. Among RAB that were isolated were *Streptomyces*, *Pseudomonas*, and *Bacillus* colonizing the roots of terrestrial orchids that have the ability of producing indole-3-acetic acid (IAA) which is an important plant growth hormone (Tsavkelova et al. 2007).

The terminology "Orchidaceae root-associated fungal endophytes" (ORAFEs) refers to endophytes that dwell within the cortical or velamen tissues of Orchidaceae roots. Numerous studies had established the existence of these endophytes in the roots of a wide variety of orchid species. A total of 13 species of endophytic fungi have been identified including, *Aspergillus flavus* (*A. flavus*) and *Trichoderma harzianum*, from the roots of *Dendrobium moniliforme* and *Dendrobium transparens*, and their discoveries indicated the presence of bioactive substances, corroborating the claim that these endophytic fungi possess antimicrobial properties that inhibits the bacterial growth (Shrestha et al. 2018). *A. flavus* is well-known for being used in the fermentation market, specifically in the production of Asian fermented foods (Chang & Ehrlich 2010). Similarly, *A. flavus* can be brought into the crop environment to help prevent preharvest contamination of crops, such as aflatoxin contamination which is linked to human sickness. The roots of epiphytic and lithophytic orchids in the genus Lepanthes were reported to harbour fungal endophytes, which were later identified as the *Xylaria* species and *Rhizoctonia*-like fungal species (Bayman et al. 1997). The habitat of orchid mycorrhizal fungi such as *Rhizoctonia* is restricted to the roots of orchids only, whereas orchid shoots are believed to contain defensive substances which deter fungal endophytes (Hadley 1982). This has suggested that endophytic microorganisms could only be found at a specific site of a plant due to different metabolic functions of different plant parts. Hence, the research could consider investigating the mechanism of action of plants which resulted in the distribution of endophytes.

ENDOPHYTES AS PLANT GROWTH PROMOTERS

Potassium Solubilization

Potassium (K) is an essential element in nutrient uptake in plants. It is also an element commonly used as fertilizer in agricultural production, as seen by the widespread use of potassium chloride fertilizer mixes (Tajer 2021). When an adequate concentration of K is supplied to plants, it improves the photo-assimilate transfer from leaves to roots and boost nitrogen use efficiency by regulating photosynthesis, carbon and nitrogen metabolizing enzyme activities, nitrate assimilation gene activities, and nitrate transport (Xu et al. 2020). Typically, soil contains higher concentrations of K compared to any nutrient. K is the seventh most prevalent element in the Earth's crust, after oxygen and silicon. In soil, the total potassium level ranges between 0.04 and 3 percent. Even though K is an abundant element in soil, only 1 to 2 percent of this element is available for plant uptake (Sparks & Huang 1985). Nevertheless, fixed potassium and structural potassium are not accessible for plant uptake, and these two forms of potassium are referred to as exchangeable and non-exchangeable forms of potassium, respectively (Mouhamad et al. 2016).

The use of chemical fertilizers has a significant negative impact on the long-term sustainability of the environment. Hence, alternative measures to chemical fertilizers are needed. Several bacteria and fungi have been shown to be able to solubilize potassium-bearing minerals and converting the insoluble K into soluble forms of K which are readily available for plant uptake, however, the exact biochemical pathways remain unexplored (Rashid et al. 2016). The manufacture and management of biological fertilizers including potassium solubilizing bacteria and fungi are alternative to chemical fertilizers which can reduce reliance on chemical fertilizers. Because of the growing interest in using endophytes to solubilize inaccessible forms of potassium, isolation and screening must be evaluated. A study developed a modified and enhanced agar plate for the process by adding an indicator dye to an Aleksandrov medium to allow better visualization of the formation of halo zones around colonies that had successfully shown a positive result (Rashid et al. 2016). The better visibility of potential K solubilizers also helped in the discovery of weak producers based on organic acid secretion in the medium and accelerated the isolation and screening process.

Phosphate Solubilization

Phosphorus (P) is a macronutrient essential for a sustainable agricultural output since it promotes optimal plant growth and productivity (Zapata & Zaharah 2002). Additionally, P is necessary for plant growth as it is involved in a number of critical plant functions such as transfer of energy in the form of ATP, enabling the process of photosynthesis, converting sugars and starches, and also the passing of biological characteristics to the next population (Sultenfuss & Doyle 1999). The majority of P in soil is present in trace amounts, and it is in the inactive state of a phosphate, which is bonded to a number of soil minerals elements that inhibited the absorption by plant (Hinsinger 2001). P has also been utilized as a fertilizer to encourage high agricultural yields, but due to the emergence of edaphic processes, P has become immobilized in soil, preventing sufficient availability for plant absorption.

P is assimilated and distributed by the root hairs, root tips, or the exterior coats of root cells, which can be aided by mycorrhizal fungi that occur in conjunction with the roots of several plants (Sultenfuss & Doyle 1999). The discovery of a phosphate-solubilizing endophyte is among the breakthroughs that have the potential to deliver an environmentally benign yet economically viable solution to phosphate deficiency. These beneficial microbes could convert insoluble P compounds to soluble P for greater uptake by plants through the hydrolysis of organic and inorganic insoluble phosphorus molecules (Kalayu 2019). Endophytes such as *Pseudomonas* are extremely effective at phosphate solubilization for plants due to their involvement in synthesizing organic acids and acid phosphatases (Rodríguez & Fraga 1999). Hence, numerous research studies have focused on assessing the ability of the endophyte in phosphate solubilization. The isolates of *Enterobacter* sp. and *Serratia* sp. have been reported to be able to solubilize P and the increased solubilization process is associated with the decrease in pH value of the media (Sánchez-Cruz et al. 2019). The results also indicated that the pH value declines during the early phases of bacterial growth, which coincides with phosphate solubilization.

Indole Acetic Acid Synthesis

Endophytes that are able to generate indole-3-acetic acid (IAA) are amongst the well-known significant plant growth-promoting traits because of their relevance in regulating key facets of plant growth and development (Fu et al. 2015). Thus, studies on exploiting the potential of endophytic microorganisms that are able to synthesize IAA has been conducted globally in hopes of finding alternatives to chemical fertilizers for sustainable agriculture. IAA is predominantly synthesized in the young shoot organs to aid its growth and stimulating vascular differentiation (Aloni et al. 2006). Li et al. (2017) compared several studies regarding the mechanism of auxin regulation in plant growth by controlling the gene expression via auxin response factors (ARFs). ARFs bind to auxin response DNA elements (AuxRE) in the promoters of auxin-regulated genes and either activate or repress transcription of these genes depending on a specific domain in the middle of the protein. The lateral root of Arabidopsis was used as a model to study the roles of hormonal signals that are responsible for regulating lateral root development (Casimiro et al. 2001). A study has reported that modification of root structure by AUX1 mutations disrupted the transportation of IAA and exogenous application of 1-napthylacetic acid recovered the *aux1* lateral root phenotype (Marchant et al. 2002). *Enterobacter cloacae* MSR1 is a plant growth-promoting endophytic bacteria isolated from the roots of Medicago sativa by culturing them in a Lauria Bertani broth supplemented with tryptophan (Khalifa et al. 2016). The tryptophan served as the precursor for IAA synthesis as plant roots tend to produce an amount of nutrients when consumed by the endophytic bacteria. Evidence have shown that IAA could act as a signaling molecule due to its mode of action that enabling efficient switching among transcriptional repression and activation of genes via auxin-dependent degradation of transcriptional repressors (Lavy & Estelle 2016). IAA has multiple functional roles which are crucial to plant growth and development. The close interaction of plant growth promoting microorganisms and its ability to produce IAA have a significant impact on the environment as well.

Siderophore Synthesis

Plants or microorganisms that grow in a low concentration of iron produce an organic substance, namely siderophores (Schwyn & Neilands 1987). Siderophores play a vital role in chelating ferric iron [FE(III)] from varied terrestrial and aquatic habitats, making it accessible to plant cells (Ahmed & Holmström 2014). In order for the siderophores to be available for the endophytic cells, they must have the ability to form complexes with essential components such as molybdenum, manganese, and carbon monoxide (Bellenger et al. 2008). However, reports on the link between endophytes that produce siderophores and plants are uncommon. However, the most frequently encountered siderophores is in crops that resulted in the induction of systemic resistance mediated by endophytic rhizobacteria (Aznar & Dellagi 2015). Endophytes may uptake Fe from the apoplast of the root when there is a high concentration of Fe in the root, as Fe(III) can be supplied to the apoplast of the root. (Abadía 1995; Kosegarten et al. 1999). The ability of endophytic bacteria *Methylobacterium* sp. in producing siderophores were observed through several bioassays including chrome-azurol agar assay test (CAS), Csáky test and Arnow test (Lacava et al. 2008). Another study reported that the siderophore producing endophytes aided the plant growth by supplying iron to the plants (Maheshwari et al. 2019). Endophytic microorganisms can produce numerous types of siderophore in nature, including Hy-

Table 1. A summary of endophytes and their known abilities.

Endophytes	Activities	References
Dyella marensis, *Collimonas pratensis*, *Luteibacter rhizovicinus*	Associated with terrestrial orchids	(Herrera et al. 2020)
Laccaria laccata	Douglas-fir ectomycorrhizal development	(Duponnois & Garbaye 1991)
Pseudomonas fluorescens BBC6	Aids the formation of ectomycorrhiza	(Deveau et al. 2007)
Fusarium sp.	Protocorm induction and seed germination	(Vujanovic et al. 2000)
Colletotrichum	Enhance plant defence mechanisms	(Scherr et al. 2014)
Strepyomyces sp., *Pseudomonas* sp., *Bacillus* sp.	Produce indole-3-acetic acid (IAA) plant growth hormone	(Tsavkelova et al. 2007)
Aspergillus flavus, *Trichoderma harzianum*	Possesses antimicrobial which inhibits bacterial growth.	(Shrestha et al. 2018)
Xylaria sp., *Rhizoctonia* sp.	Contain defensive substances	(Hadley 1982)
Pseudomonas sp, *Enterobacter* sp., *Serratia* sp.	Phosphate solubilization activity	(Kalayu 2019; Sánchez-Cruz et al. 2019)
Enterobacter cloacae MSR1	Plant growth promoting properties	(Marchant et al. 2002)
Methylobacterium sp.	Siderophores production	(Lacava et al. 2008)

droxymate and Catecholates which are required in small amounts by plants to enrich the yield of crops (Pahari et al. 2017). Siderophores are often overlooked in conventional farming which utilized chemical fertilizers that focus on supplying the NPK nutrients, further studies that investigate the role and mechanism of action by different siderophores can create a deeper understanding.

CONCLUSIONS

The agriculture sector has long heavily relied on chemical fertilizer. The negative impact of such practice is huge towards the environment as well as to human well-being in future. This review article has provided insights towards the potential of plant growth promoting microorganisms isolated from Orchid. The microorganisms carry potassium, phosphorus as well as other bioactivities towards plant growth and development. These plant growths promoting microorganisms can be utilized to enhance the crop yield and reduce dependency on chemical fertilizers. The mode of interactions and mechanism between plant growth promoting microorganisms and plant can be further explored in future studies to increase the understanding in this aspect.

AUTHOR CONTRIBUTION

Conceptualization, J.A.G. and L.P.W.G.; formal analysis and investigation, B.L.J. and R.J.; resources, X.X.; data curation, R.J.; writing—original draft preparation, L.P.W.G. and B.L.J.; writing—review and editing, J.A.G., L.P.W.G., B.L.J., R.J.; supervision, J.A.G.; project administration, J.A.G. All authors have read and agreed to the published version of the manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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